

Resilience to Changing Climate and Wildfire  
in Subalpine Conifer Forests of Greater Yellowstone

By

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In memory of Olive. You entered my life when I began graduate school and left it at the end. I  
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**Abstract**

Resilience to Changing Climate and Wildfire in  
Subalpine Conifer Forests of Greater Yellowstone

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Climate and disturbance regimes are rapidly changing in earth's forests, and these trends are expected to continue through the 21<sup>st</sup> century. It remains unresolved whether and where forests will absorb increased perturbations without changing qualitatively and where forest resilience might erode. This dissertation provides a foundation to begin addressing these uncertainties. I combined field observation, experiments, and process-based simulation to study effects of changing climate and wildfire on postfire tree regeneration and forest resilience in Yellowstone National Park, the largest intact wildland area of the contiguous United States. Chapter 1 quantifies effects of ecological filters on a colonizing cohort of aspen. These aspen trees established from seed after the 1988 fires and survived at higher elevations than their prefire distribution. I then conducted a long-term field experiment and shorter controlled-environment experiment to determine how temperature and soil moisture consistent with 21<sup>st</sup>-century projections may alter postfire seedling establishment of two widespread conifers (Chapter 2). In chapters 3 and 4, I used a forest simulation model to test multiple mechanisms of regeneration failure and to explore how suppression may alter 21<sup>st</sup>-century fire and forests. Long-term study of colonizing aspen demonstrated how wildfire can catalyze rapid shifts in tree-species distributions. Aspen seedlings were initially favored at lower elevations close to their

prefire distribution. By 25yrs postfire, aspen was favored to survive at higher elevations, likely due to warming. From the experiments, it appears postfire drought may be a powerful force for change in subalpine forests because regeneration was drastically reduced under hotter-drier conditions. Simulations, where multiple climate-fire drivers could be considered over longer periods, however, indicate the potential for remarkable resilience. Regeneration failure was the exception, not the rule. Suppression of fire also had little impact on 21<sup>st</sup>-century fire or forests. Collectively, this research demonstrates that multiple streams of quantitative inquiry are necessary to better resolve how changing climate and disturbance will alter forests. Management steps could be taken to bolster vulnerable forests (e.g. reseedling after fires), if mechanisms of change are understood. However, forest-management strategies should not discount the inherent resilience of the system.

## Introduction

Forests have often changed slowly in response to environmental variation over the past several thousand years (Whitlock 1993, Higuera et al. 2009). Because of their stability, forests have long served as a social-ecological spine: They are a foundational component of the earth system (Chapin et al. 2000, Bonan 2008) and provision critical ecosystem services to society (Turner et al. 2013, Seidl et al. 2016). However, the rate of change in forests is accelerating with warming and increased disturbance (Gauthier et al. 2015, Millar and Stephenson 2015). Alaskan boreal forests that were dominated by black spruce for millennia are now shifting abruptly to deciduous dominance after unusually severe wildfires (Johnstone et al. 2010). In California, an extreme drought has caused forest mortality to increase by an order of magnitude – from tens to hundreds of trees km<sup>2</sup> in just four years (Young et al. 2017).

It appears that recent change in forests may only be a bellwether of what to expect over the next century (Trumbore et al. 2015, Reyer et al. 2015, Ghazoul et al. 2015, Seidl et al. 2017). Projections of climate and disturbance regimes for many forests suggest conditions could occur during the 21<sup>st</sup> century that are unlike anything experienced in the past 10,000 years (Westerling et al. 2011, Kelly et al. 2013). Recent trends and future projections raise the question: Where will earth's forests remain resilient to changing climate and disturbance and where and why might forests change fundamentally?

Changes in forests across broad scales will likely emerge from multiple environmental drivers acting on local-scale processes, such as individual tree growth and survival, competition between individuals, seed dispersal, and seedling establishment (Peters et al. 2004, 2007, Turner 2010). Forests are hierarchically structured systems. Cross-scale interactions are common



because the behavior of individual elements at lower levels of organization, are constrained by, and shape pattern and process at higher levels of organization (O'Neill et al. 1989, Filotas et al. 2014, Messier et al. 2015, Rose et al. 2017). The fate of individual trees influences the fate of the forest. Novel climate and disturbance could also initiate non-linear feedback loops in forests that accelerate or dampen rates of change (May 1977, Walker et al. 1981, Lenton 2013).

Cross-scale interactions and nonlinear feedbacks make it very difficult to anticipate how forests will respond to environmental change because of the complex and contingent nature of outcomes (Peters et al. 2004, 2007). For example, the consequences of a severe drought can depend on forest successional stage. A mature forest may prove resilient, as adult trees can tolerate a wide range of environmental conditions, but resilience could be exceeded in a young forest where tree seedlings are quite sensitive (Jackson et al. 2009, Bell et al. 2014). Any one scientific approach is insufficient. Instead, multiple ways of knowing, such as field observation, experiments, and simulation are required (Carpenter 1998, Seidl 2017).

Warming and drying trends during spring and summer in conifer forests of the western United States are leading to marked increases in the frequency and size of wildfires (Kasischke and Turetsky 2006, Westerling et al. 2006, Littell et al. 2009, Westerling 2016, Abatzoglou and Williams 2016). The number of large fires and area burned in those fires have increased 556% and 1,271% greater since the 1970s (Westerling 2016). Climate and fire trends are projected to continue during the 21<sup>st</sup> century (Balshi et al. 2009, Westerling et al. 2011).

Wildfires in widespread subalpine forests account for a sizeable percentage of the increased burning in the western US (Westerling 2016). Subalpine fires are generally large ( $10^2$ - $>10^5$  ha), historically infrequent (100-300yrs), severe (killing most trees) (Romme and Despain

1989, Turner et al. 1994, Loehman et al. 2018), and strongly limited by climate, rather than fuel (Bessie and Johnson 1995, Rollins et al. 2002, Barbero et al. 2015). Forest regeneration after large severe fires will likely be a 21<sup>st</sup>-century resilience linchpin in subalpine forests because regeneration dynamics during the first few years postfire shape stand structure and tree-species composition for decades to centuries (Kashian et al. 2005).

Forest resilience could be compromised during the postfire regeneration phase if (1) fires begin to burn frequently enough that trees are consumed before producing cones, (2) fires burn large enough that seed delivery is reduced, or (3) seedlings are killed by drought (Johnstone et al. 2016, Turetsky et al. 2017, Stevens-Rumann et al. 2018). However, it is not particularly easy to determine whether and how postfire tree regeneration could be compromised. Very large burned patches and short-interval fires remain unusual, and so there is often insufficient sample size to quantify their effects in the field. People have also drastically altered the fire regime in many western forests, which confounds effects of climate change and increasing disturbance with land use legacies (Schoennagel et al. 2004, 2017, Stephens et al. 2013, 2016, Balch et al. 2017).

Yellowstone National Park in northwestern WY, is a rare natural baseline for subalpine forests of the western US because human impacts have been less pronounced (Turner et al. 2016a) and because it is one of the best studied forest ecosystems on earth (Turner et al. 1994, 1997, 2004, 2016b, Romme et al. 1995, 2005, Donato et al. 2016). This makes it a valuable place to explore effects of changing climate and fire on forest resilience. Yellowstone is the largest intact wildland area in the contiguous US. It was designated a national park in 1872. Even before the designation, however, Yellowstone was far from the trodden path, due to the remote location and harsh climate (Schullery 1997). Intact subalpine lodgepole-pine forests cover 80% of the

park (Despain 1990). These forests have experienced large stand-replacing wildfires every 100 to 300 years during the Holocene (Millspaugh et al. 2000). In fact, the iconic 1988 fires that burned roughly 600,000 ha are said to have ushered in the large-fire era in the western US (Romme et al. 2011). Evidence suggests that past climate variation strongly shaped patterns of forest structure and tree-species composition in Yellowstone (Whitlock 1993).

Here, I use multiple streams of quantitative inquiry to better resolve how changing climate and fire may alter postfire regeneration and forest resilience in subalpine forests of Yellowstone. In Chapter one, I combined long-term data with extensive field observation to quantify the effects of ecological filters on a colonizing cohort of trembling aspen (*Populus tremuloides*). These aspen trees established from seed after the 1988 wildfires and have survived, far from, and at much higher elevations than their prefire distribution, likely due to warming. I then conducted a four year *in situ* and shorter controlled-environment experiment to evaluate how increased prevalence of drought may alter postfire regeneration of lodgepole pine and Douglas-fir, another widespread conifer in Yellowstone (Chapter two).

Mechanistic understanding of individual environmental drivers, such as drought, is important for resolve how 21<sup>st</sup>-century forests may change, but multiple interacting drivers are likely to actually shape outcomes. I then used a next generation process-based forest simulation model to quantify effects of changing climate and fire at stand and landscape scales. In chapter three I conducted a factorial simulation experiment where I determined the combinations of changing climate, fire frequency, and distance to seed source that cause regeneration failure of Douglas-fir and lodgepole pine. In chapter four, I synthesized across the other three chapters and additionally considered the impacts of fire managers. In a forested subalpine landscape, I

evaluated how letting fires burn (vs. suppressing them) under average weather conditions alters 21<sup>st</sup>-century fire and forests.

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**Chapter 1 – Shifting ecological filters mediate postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone**

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## Abstract

Determining how ecological filters (e.g., climate, soils, biotic interactions) influence where species succeed in heterogeneous landscapes is challenging for long-lived species (e.g., trees), because filters can vary over space and change slowly through time. Stand-replacing wildfires create opportunities for establishment of tree-species cohorts and can catalyze rapid shifts in where species occur, facilitating unique opportunities for long-term study. We quantified effects of multiple ecological filters on a colonizing cohort of aspen (*Populus tremuloides*) that established from seed throughout burned lodgepole pine (*Pinus contorta* var. *latifolia*) forests after the 1988 fires in Yellowstone National Park (Wyoming, USA) to ask: (1) How have aspen presence, density, and size varied across the postfire landscape, and what filters explain these spatial and temporal patterns? (2) How do aspen above-and belowground biomass vary with postfire lodgepole-pine density? Aspen persisted to postfire year 25 in 58% of the plots in which aspen were present in postfire year 11 ( $n = 45$ ), and mean stem density declined from 522 to 310 stems  $\text{ha}^{-1}$ . Mean aspen height doubled (from 29 to 59 cm) over this period. Ecological filters related to climate, competition, herbivory, and soils all differentially affected aspen presence, persistence, and size. Growing season temperature, inter-specific competition, and herbivory also changed through time, altering their effects on the colonizing cohort, and shifting where on the landscape aspen persistence and growth were ultimately favored. Eleven years postfire, aspen was favored at warmer, low elevations; ungulate browsing strongly constrained aspen heights; and competition was unimportant. By 25-years postfire, temperatures warmed nearly  $1^{\circ}\text{C}$ , and aspen were more likely to persist at cooler, high elevations. Browsing pressure declined, as ungulate populations decreased during this time, but aspen height and basal diameters were

constrained by dense, rapidly growing postfire conifers. Landscape mosaics of ecological filters shift over space and time and can facilitate or constrain the persistence and growth of colonizing species. Long-term study of post-disturbance colonizing cohorts uniquely reveal how species are responding to real-time environmental change in heterogeneous landscapes, which will help us better anticipate 21<sup>st</sup> century species distributions and abundances.

*Keywords:* Cervus elaphus; climate change; natural disturbance; Northern Rocky Mountains; range expansion; species distribution

## 1. Introduction

As environmental change accelerates, it is critical to determine how multiple ecological filters (e.g., climate, topography, soils, disturbance, competition, and herbivory) determine where species establish and thrive in landscapes (Walther *et al.* 2002; Thomas *et al.* 2004; Bellard *et al.* 2013). However, identifying the influence of ecological filters on species' success is challenging because filters often vary spatially and may change over time (Venn *et al.* 2011; Lawler *et al.* 2015). Particular ecological filters (e.g., disturbance, climate, competition, and herbivory) can also differentially affect establishment, persistence, or performance of a species (Bunker & Carson 2005), and thus, relative strengths of ecological filters will vary across the life history stages of an organism (Keeley, Fotheringham, & Baer-Keeley 2005; Masaki *et al.* 2005; Nogueira, Costa, & Castilho 2011; Lasky *et al.* 2013). For example, landscape heterogeneity may govern propagule supply and affect initial species presence and density, but local topographic conditions might drive subsequent persistence and growth (Neilson *et al.* 2005). Due to these complexities, tracking the fate of colonizing cohorts in heterogeneous landscapes could yield powerful insights into how species distributions are shaped over space and time.

In forests, opportunities for cohort studies are rare because trees can establish at different times during succession and persist for decades (Whitlock 1993; Hughes *et al.* 2013). However, stand-replacing disturbances allow for establishment of species cohorts, and disturbances may also facilitate expansion beyond previous patterns of occurrence if environmental conditions have been changing (Johnstone *et al.* 2010; Turner 2010; Ettinger, Ford, & HilleRisLambers 2011; Mann *et al.* 2012). In subalpine and boreal conifer forests, high-severity wildfires initiate a pulse of postfire tree regeneration, and resulting tree cohorts offer opportunities to evaluate



filters that influence their success over time (Romme 1982; Turner *et al.* 1997; 2004; Johnstone & Chapin 2006a). Following the extensive 1988 fires in Yellowstone National Park (Wyoming, USA), a cohort of trembling aspen (*Populus tremuloides*) seedlings established in burned lodgepole pine (*Pinus contorta* var. *latifolia*) forests. These colonizing aspen were found far from (> 15 km) and at higher elevations (> 500 m) than prefire aspen stands (Turner *et al.* 2003; Romme, Turner, & Tuskan 2005). Excavation and genetic analyses confirmed aspen were seedlings (not resprouts), and 92% of stems were genetically distinct (Stevens *et al.* 1999; Romme, Turner, & Tuskan 2005). This widespread recruitment event provided an exceptional opportunity to investigate 25 years of development in a colonizing tree cohort.

Aspen is the most widespread native tree species in North America (Fowells 1965), ranging from northern Mexico to northern Alaska, and has a flexible life-history strategy (Barnes 1975; Jones 1985; Rogers, Eisenberg, & St. Clair 2013). Aspen are often long-lived because individuals (genets) can produce multiple generations of genetically identical stems (ramets) from a common root system (Day 1944). Aspen also reproduce sexually, and seed dispersal followed by recruitment is necessary for distribution shifts. Aspen seedling recruitment had been considered rare in the Rocky Mountains because a narrow range of conditions are required for germination and establishment. Yet, a growing number of studies report establishment following stand-replacing fires (Kay 1993; Quinn & Wu 2001; Turner *et al.* 2003; Landhäusser, Deshaies, & Lieffers 2010; Fairweather, Rokala, & Mock 2014; Krasnow & Stephens 2015). Aspen seedling recruitment events appear to be occurring more frequently at higher elevations, facilitating their upslope expansion as climate warms (Turner *et al.* 2003; Kashian, Romme, & Regan 2007; Landhäusser, Deshaies, & Lieffers 2010). Concomitantly, recent widespread

mortality of mature aspen, particularly at southern latitudes and low elevations (Worrall *et al.* 2013), has heightened interest in understanding shifting distributions (Frey *et al.* 2004; Hogg, Brandt, & Michaelian 2008; Hanna & Kulakowski 2012; Bell, Bradford, & Lauenroth 2014; Yang *et al.* 2015). Thus, identifying ecological filters that facilitate or constrain aspen establishment is critical for anticipating shifts in their presence and abundance (Krasnow & Stephens 2015). Long-term study of a postfire seedling aspen cohort could also strengthen our understanding of how spatially and temporally shifting ecological filters dictate where colonizing species successfully establish and grow.

During early postfire years (i.e., within the first decade), ecological filters affecting initial presence and density of colonizing tree species are related to fire severity and propagule pressure. In Yellowstone, postfire aspen establishment depended on occurrence of fire and proximity to seed source, though seedlings were found as far as 15 km from mature aspen. Fine-scale (< 200 m) variation in aspen density was primarily related to elevation, with greater densities at lower elevations, while across broad scales (> 1,000m), initial aspen densities increased with burn severity (Turner *et al.* 2003). Establishment, density, and growth of colonizers will also be affected by climate, particularly for trees that have not developed sufficient root systems to survive inhospitable conditions. However, early postfire competition is likely minimal, as wildfires release previously unavailable resources and reduce plant uptake (Smithwick *et al.* 2005a).

Once colonizers establish, other filters, such as soil conditions and biotic interactions (including inter-specific competition and herbivory) are likely to become increasingly important determinants of persistence and growth (Kaye, Binkley, & Stohlgren 2005; Cavard *et al.* 2011;

Seager; Eisenberg & St. Clair 2013). Benefits of soil fertility for aspen growth are well documented (Hobbie & Chapin 1998; Smith *et al.* 2011) and, in Yellowstone, postfire colonizing aspen grow very slowly because soils are highly infertile (Romme, Turner, & Tuskan 2005). As growth of postfire conifers accelerates, competition with aspen for water, nutrients, and light may intensify (Romme, Turner, & Tuskan 2005), altering aspen stem and root growth and increasing aspen mortality (Casper & Jackson 1997). Aspen are a nutrient-rich resource for herbivores (DeByle 1985), and browsing by ungulates such as elk (*Cervus elaphus*) can limit ramet (Romme *et al.* 1995; Rogers & Mitanck 2014) or seedling heights (Romme, Turner, & Tuskan 2005). Browsing effects depend on ungulate behavior and population size, which varies over time; a substantial decline in Yellowstone elk numbers between 1997 and 2014 (Smith *et al.* 2015) has been linked to increased aspen-ramet heights in mature stands (Painter *et al.* 2014).

We quantified how multiple ecological filters have affected the success of a colonizing seedling-aspen cohort that established after the 1988 Yellowstone fires. We asked: (1) How have aspen presence, density, and size varied across the postfire landscape, and what ecological filters explain these spatial and temporal patterns? We hypothesized climate and elevation would serve as primary filters of aspen presence and density, and soil fertility, competition with conifers, and ungulate browsing would influence aspen size. We also hypothesized climate and elevation would become less important for predicting aspen presence over time, and that declining numbers of Yellowstone elk would correlate with aspen release, but competition with conifers would increasingly constrain aspen size. To further characterize how competition with conifers might influence aspen stem and root growth, we excavated colonizing aspen 26 years postfire to ask: (2) How does aspen above- and belowground biomass vary with lodgepole pine density? We

hypothesized that 26 years postfire, aspen would have begun developing clonal structure, thus allocating more biomass to lateral roots than stems. We also expected biomass allocation to vary with lodgepole pine density, but with two alternative patterns possible. If nutrients or water limit growth, aspen would allocate relatively more biomass to roots than stems in high-density lodgepole pine stands. If light limits growth, aspen would allocate relatively more biomass to stems than roots.

## **2. Materials and methods**

### *2.1 Study area*

Located in northwestern WY, USA, Yellowstone National Park is approximately 9,000 km<sup>2</sup> (Fig. 1). Our study focused on the subalpine central plateau that covers most of the park and is dominated by coniferous forest, primarily lodgepole pine (Despain 1991). Climate is cool with mean temperatures of -9 °C in the winter and 12 °C in the summer (Western Regional Climate Center 2014). An extensive winter snow pack develops at high elevations, increasing growing-season moisture availability. Soils include highly infertile, rhyolite derived substrates, slightly less infertile andesite substrates, and pockets of glacial/lake detrital deposits. In 1988, approximately 174,000 ha of forest burned as stand-replacing fire on the central plateau (Turner, Romme, & Tinker 2003; Turner *et al.* 2004). Before the 1988 wildfires, aspen occupied 1.4% of Greater Yellowstone (Brown *et al.* 2006) and were primarily present in low-elevation montane forests (Despain 1991). Aspen were present only occasionally on the central plateau, restricted to talus slopes, where conifer forests were not present (Turner *et al.* 2003).

### *2.2 Field sampling*

*2.2.1 Aspen presence and density.* During summer 2012, we resampled 72 widely distributed 0.25-ha permanent plots (Fig. 1) in lodgepole pine forests that burned in 1988 as stand-replacing fire. These plots were established and sampled in 1999 (Turner *et al.* 2004), and we followed the same sampling protocols. Briefly, we tallied the number of postfire aspen and conifers by species in three parallel 50-m x 2-m belt transects oriented due north and separated by 25 m. Additionally, we recorded the basal diameter of 25 lodgepole pines.

*2.2.2 Aspen size.* During summer 2013, we resampled 21 smaller permanent plots (Romme, Turner, & Tuskan 2005) (Fig. 1). Plots were established in 1996 and were of variable size to encompass at least 10 aspen seedlings. Aspen height and basal diameter, evidence of ungulate browsing, and local lodgepole pine density had previously been measured in 1996, 1997, 1998, and 2000 (see Romme, Turner, & Tuskan 2005), and we followed the same protocols. Briefly, we sampled along a transect of 10 to 20 m in length, measuring aspen size on both sides and counting lodgepole pines within a 2 to 4-m belt (depending on stand density). We examined leaders and branches for browsed buds and twigs to determine percent of individuals browsed. Three mineral soil samples were collected using a 15-cm long PVC corer. Soils were sieved, composited by site, and oven dried at 60 °C to constant mass. Soils were analyzed for % total soil nitrogen (N) (micro Kjeldhal procedure), soil pH (measured in water), % organic matter (determined using dry combustion), and available phosphorous (Bray P1 extract) by the University of Wisconsin Soil and Plant Analysis Laboratory, Madison, WI, USA (UW SPAL 2013).

*2.2.3 Aspen above- and belowground biomass.* Eighty individual aspen had been excavated in 1996 to document clonal structure and to calculate above- and belowground

biomass ratios (see Romme, Turner, & Tuskan. 2005). To estimate current above- and belowground biomass ratios, in summer 2014, we excavated 10 aspen at six plots (approximately two aspen per plot) using hand tools (Fig. 1). Although a sample size of 10 is small, it was logistically infeasible to harvest additional trees. Plots spanned a range of lodgepole pine densities (500-33,000 lodgepole pine ha<sup>-1</sup>) tallied along a 20-m x 4-m belt transect. At each site, we selected one or two of the largest aspen individuals, separated by at least 15 m. We first measured height and basal diameter of the dominant stem. We then excavated all lateral and sinker roots until they were too small to follow ( $\leq 2$  mm diameter). We measured the length of each lateral root, counted all ramets that emerged from each lateral root, and recorded their height and basal diameter. All biomass was harvested and separated into three components: aboveground woody biomass, leaves, and belowground biomass. Biomass was dried at 70°C to constant mass and dry mass was recorded. Cross sections from each dominant stem were collected to determine stem ages. Stem cross sections were finely sanded (400 grit) and tree rings were counted with an Olympus SZ-61 6.7x-45x stereo microscope (Stokes & Smiley 1996).

### *2.3 Ecological filters*

Covariates related to climate, topographic conditions, and competition with lodgepole pine were obtained for each plot (Appendices A, B). Gridded temperature and precipitation PRISM data (4-km resolution) were used to characterize climate for the 72 aspen presence-density plots and the 21 aspen size plots (PRISM Climate Group 2014). Mean growing season (April-September) temperature and mean annual precipitation were calculated for the decade prior to each sampling year. Topographic variables included elevation and substrate, which was grouped into four categories, according to physical characteristics of the soil and their expected

effect on vegetation (Turner *et al.* 2004). Ordered from least to most fertile, based on nutrient status and water-holding capacity (Turner *et al.* 2004), substrate categories included rhyolite till, which occurs on uplands and is derived from rhyolite-based glacial till; rhyolite glacial, located on glacial outwash plains; rhyolite low-base saturation, occurring on lake plains and derived from rhyolite-based glacial rubble; and andesite, located in glacial valleys and alluvial fans. The andesite category includes soils derived from andesite, as well as alluvial, lake-based, and organic deposits. As an indicator of competition with lodgepole pine, annual aboveground net primary production (ANPP) was calculated for each of the 25 trees using allometric equations specific to the region and tree age (Turner *et al.* 2004; Copenhaver & Tinker 2014). Annual stand-level ANPP was then determined by multiplying mean tree ANPP by tree density and reported as  $\text{Mg ha}^{-1} \text{ yr}^{-1}$  (Turner *et al.* 2004).

## 2.4 Data analysis

*2.4.1 Aspen presence and density.* Presence of aspen seedlings in 1999 and persistence to 2012, given aspen presence in 1999, were analyzed using logistic regression. We also used multiple linear regressions to analyze aspen seedling density when they were present in 1999 and when aspen persisted from 1999 to 2012. For all regressions, variables were log transformed as necessary and multicollinearity was evaluated using variance inflation factor cutoff of less than five. Aspen seedling presence and density were modeled as a function of climate (mean growing season temperature and mean annual precipitation), topo-edaphic conditions (elevation and substrate), and conifer competition (lodgepole pine ANPP) (Appendix A). Exhaustive model selection (Burnham and Anderson 2002) was conducted using the R package MuMIn (Barton

2015). Coefficients from all top models ( $\Delta \text{AICc} < 2$ ) are presented. All analyses were conducted in R statistical software (R Core Development Team 2010).

*2.4.2 Aspen size.* Aspen height and basal diameter in 1996, 2000, and 2013 were modeled using multiple linear regressions, as for aspen density. Soil organic matter, total soil N, and available phosphorous were highly correlated. To avoid collinearity, we conducted a factor analysis on the 1996 soil data with varimax rotation (Revelle 2015). Total N loaded most strongly on factor one. Soil pH loaded most strongly on factor two (Appendix C). Thus, total N and soil pH were retained in analyses. Additional independent variables included climate variables (average growing season temperature and average annual precipitation), and conifer competition (lodgepole pine density) (Appendix B). We used lodgepole pine density instead of ANPP, because lodgepole pine basal diameters necessary for applying allometric equations were not measured in 1996 or 2000, but lodgepole pine density is positively correlated with stand-level ANPP (Turner *et al.* 2004). Ungulate browsing could not be included in regressions because browsing was uniformly high in 1996 and uniformly low in 2013, providing little variation among sites for regression.

*2.4.3 Aspen above- and belowground biomass.* Aspen biomass allocation was quantified by calculating two ratios: (1) aboveground woody biomass to belowground biomass, and (2) belowground biomass to whole plant biomass (belowground + aboveground woody + leaf biomass). One plot was excluded from biomass ratios as we were unable to harvest the entire taproot that extended below an immovable rock. Because root length may be a good indicator of nutrient and water acquisition capabilities (Chapin, Matson, & Vitousek 2012), we calculated four other ratios: dominant stem height to median lateral root length, mean lateral root length,



and max lateral root length, and sum of stem heights (dominant stem + ramets) to sum of lateral root lengths. The site excluded from biomass ratios was included in length ratios because we were able to collect all lateral roots of that individual, allowing for rigorous comparison. Relationships between all ratios and lodgepole pine density were evaluated using Kendall's Tau, which is a correlation coefficient appropriate for data with tied ranks.

### 3. Results

#### 3.1 *Aspen presence and density*

In 1999, aspen were present at 45 of 72 plots (62.5 %). Probability of aspen presence in 1999 increased strongly with growing season temperature (Table 1 A, Fig. 2). Aspen were also more likely to be present in plots where annual precipitation and lodgepole pine ANPP were higher (Fig. 2). Aspen were less likely to occur at high elevations (Fig. 2) and on infertile rhyolite-glacial soil, as compared to andesite soils. Aspen seedlings persisted from 1999 to 2012 at 26 of the 45 plots (58 %). Effects of growing-season temperature and elevation switched directions from 1999 (Table 1 A, Fig. 2). Aspen were more likely to persist from 1999 to 2012 at *higher* elevations and *cooler* temperatures.

In the 45 plots where aspen were present in 1999, mean density was  $522 \pm 140$  stems  $\text{ha}^{-1}$ . In the 26 plots where aspen persisted to 2012, mean density declined to  $310 \pm 147$  stems  $\text{ha}^{-1}$ . In 1999 and 2012, aspen density increased with growing season temperature (Table 1 B, Appendix D), though models explained little of the variation ( $\text{adj. } R^2 \leq 0.14$ ).

#### 3.2 *Aspen size*

Mean aspen height was similar in 1996 ( $29.3 \pm 0.8$  cm) and 2000 ( $31.2 \pm 1.0$  cm), then nearly doubled by 2013 ( $58.9 \pm 2.6$  cm) (Fig. 3 A). The tallest aspen recorded in 1996 was 92.5

cm; in 2013, the tallest aspen was 323 cm. Ungulate browsing declined across the three study periods. Eighty-six percent of stems showed evidence of browsing in 1996, but only 2.6% of stems were browsed in 2013. Across all three sampling periods, aspen heights were related to soil pH, with taller aspen trees growing in more basic soils (Table 2 A). Total soil N declined markedly between 1996 and 2013 (between eight and 25 years postfire, coinciding with rapid growth of lodgepole pine), and total N was important for explaining aspen heights (Fig. 4). In 1996, aspen trees were shorter in plots with the highest total soil N ( $> 0.25\%$ ). As total N declined over time, the relationship switched, and aspen height increased with total N in 2013.

Mean aspen basal diameter increased from  $7.2 \pm 0.2$  mm in 1996 to  $9.7 \pm 0.4$  mm in 2013 (Fig. 3 B). In 1996, aspen basal diameters were larger in more basic soils and at plots where growing season temperature was warmer (Table 2 B) and these same relationships strengthened by 2000 (Table 2 B). Aspen basal diameters in 2013 were larger at plots with higher total soil N (Fig. 4) and more basic soils, and smaller at sites with high lodgepole-pine densities (Fig. 4). The amount of variance explained in both height and basal diameter models increased substantially in the later sampling periods (Table 2).

### *3.3 Above- and belowground biomass*

All ten excavated aspen had produced lateral roots by 2014, as compared to half of the plants excavated in 1996 (Romme, Turner, & Tuskan 2005), and seven of the aspen in 2014 supported ramets (Table 3). Forty percent of whole plant biomass was in roots (Table 3), similar to postfire aspen excavated in 1996 (Romme, Turner, & Tuskan 2005). Lodgepole pine density was uncorrelated with aboveground-to-belowground biomass ratio and belowground-to-whole plant biomass ratio (Kendall's Tau= 0.12 and -0.18, respectively  $P > 0.10$ ). However, lodgepole-

pine density was positively correlated with all stem-height to root-length ratios (Kendall's Tau = 0.44 to 0.58,  $P = 0.08$  to  $0.02$ ) (Fig. 5). Height of the dominant stem was greater than length of lateral roots for aspen in high- vs. low-density lodgepole pine stands.

#### 4. Discussion

Our long-term analyses of a colonizing postfire seedling aspen cohort in Yellowstone illustrate how disturbance interacts with shifting ecological filters to influence landscape patterns of species occurrence and performance over time (Table 4). Fire set the stage for aspen seedling establishment; aspen only recruited in areas that burned severely, and initial postfire seedling densities decreased with distance to mature aspen (Turner *et al.* 2003; Brown *et al.* 2015). In subsequent years, aspen grew slowly, with the tallest aspen only reaching 3.2 m after 25 years (appendix E). Subsequently, ecological filters including climate, competition, herbivory, and soils differentially affected aspen presence, persistence, and size. Several filters (growing season temperature, competition, herbivory) also changed through time, altering their effects, and shifting where on the landscape aspen persistence and growth were favored. Many of these effects would have been missed without long-term study (Table 4) which could lead to misinformed conclusions about shifting aspen distributions in Yellowstone.

Temperature has warmed in Yellowstone since the 1988 fires, and this warming appears to have already affected the geographic distribution of postfire aspen (Table 4). Initially, differences in temperature across elevation gradients favored postfire aspen establishment at lower-elevation sites that aligned more closely to the pre-fire distribution of mature aspen in Yellowstone. This was likely because the colder temperatures and deeper snowpacks at higher elevations limited aspen survival and growth (Romme, Turner, & Tuskan 2005; Krasnow &

Stephens 2015). However, growing season temperatures have since increased nearly 1°C among our plots. This recent warming appears to have been sufficient for aspen to persist to 2012 at elevations substantially above its prefire distribution, suggesting that temperature limitation has been relaxed at the higher elevations and perhaps as even increased at lower elevations.

Competition with postfire lodgepole pine had little effect on aspen survival and growth during the first decade postfire (Romme, Turner, & Tuskan 2005), but effects of competition on aspen size were evident after 25 years (Table 4). Competition with conifers is a key driver of aspen recruitment, survival, and growth throughout the Rocky Mountains (Kaye, Stohlgren, & Binkley 2003; Calder, Horn, & St. Clair 2011, Calder & St. Clair 2012), and our data suggest lodgepole pine contributed to nutrient and light limitations. Young lodgepole pines grow rapidly and are now larger than aspen, reaching heights of 3-4 m, with some >6 m (Copenhaver & Tinker 2014). Dense young lodgepole pine forests are strong N sinks (Turner *et al.* 2009), and soil inorganic N declines with lodgepole pine density (Smithwick *et al.* 2009; Turner *et al.* 2009). Soil N has declined over time in our plots, and the relationship between aspen size and soil N switched direction. Soil nitrate and ammonium concentrations increase after fire (Smithwick *et al.* 2005b, Turner *et al.* 2007), and neither aspen nor lodgepole pine were likely N limited in early postfire years (Romme *et al.* 2009). Declining soil N availability over time may have contributed to smaller aspen stature in high-density lodgepole pine stands. Additionally, smaller basal diameters of aspen in high-density lodgepole pine stands are consistent with the increased ratio of stem height to root length. Although belowground biomass remained a relatively consistent proportion (~40%) of total plant biomass over time, aspen in dense

lodgepole pine stands elongated their dominant ortet stem more than their lateral roots, suggesting competition for light is also important (Frey *et al.* 2003).

Herbivory on postfire aspen declined drastically over time, and this surely has contributed to aspen height growth (Table 4). Ramet heights in mature aspen stands on Yellowstone's northern winter range have also increased markedly (Painter *et al.* 2014). Elk seek out aspen, and winter browsing has been high for many years on the northern range (Romme *et al.* 1995; Ripple & Larson 2000; Kimble *et al.* 2011). Although our study area is on elk summer range, we also had observed very high herbivory rates on aspen seedlings during the early 2000s. Nearly 90% of stems were browsed (Romme, Turner, & Tuskan 2005). Elk habitat selection appears to not be influenced by fire (Wan *et al.* 2014). Even high-density postfire lodgepole pines and dense coarse down wood did not deter elk from finding and browsing seedling aspen (Forester *et al.* 2007). Following the 1995 reintroduction of wolves (*Canis lupus*), elk habitat selection shifted to higher elevations and more forested habitat, particularly, burned forest (Mao *et al.* 2005). Thus, browsing on aspen in postfire lodgepole pine forests was likely at its highest level during the first 15 years after fire. Since, predation on elk by wolves, grizzly bears (*Ursos horribilis*), and cougars (*Puma concolor*); harvest by hunters outside Yellowstone; and environmental change have resulted in fewer elk (Creel *et al.* 2007; Eberhardt *et al.* 2007, White *et al.* 2011; Christianson & Creel 2014). The Yellowstone elk population declined from approximately 15,000 animals in 1997 to 5,000 in 2014 (Smith *et al.* 2015).

It is notable that the central plateau of Yellowstone is not the most hospitable environment for aspen, and they grow slowly (Appendix E). After 25 years, many aspen were still less than one meter tall. Given poor soils derived from volcanic substrate (Despain 1991), it

is not surprising that aspen presence and size were related to measures of soil fertility, consistent with other studies (Romme, Turner, & Tuskan 2005; Smith *et al.* 2011). Heterogeneity in topographic conditions and microclimate within the landscape will likely continue to provide sites where aspen can survive.

Aspen density was not well explained by predictor variables included in our models. This may be because stem density is the net effect of two opposing processes – mortality and ramet production – that likely respond to different drivers. Following establishment, conceptual models predict strong intraspecific competition will lead to high early mortality in seedling cohorts of predominantly clonal species (Eriksson 1992). Declining aspen presence and stem density on the central plateau reveals ongoing mortality. However, ramet production by genets that survived in favorable locations or outcompeted other individuals for resources (Frey *et al.* 2003) may counter mortality-driven declines in stem density.

What do our findings suggest for the future of aspen in the Rocky Mountains? Warming is expected to continue and fire frequency will likely increase during the 21<sup>st</sup> century (Westerling *et al.* 2011), which could favor aspen persistence and expansion. In the northern Rocky Mountains, climate suitable for aspen is projected to shift 750 meters upward in elevation by the end of the 21<sup>st</sup> century (Rehfeldt, Ferguson, & Crookston 2009), and drought has already increased mortality and decreased recruitment in marginal portions of the species' current distribution (Worrall *et al.* 2013). Disturbances that create suitable sites for aspen establishment from seed could play a central role in facilitating upslope expansion of the species (Landhäusser, Deshaies, & Lieffers 2010; Kulakowski, Kaye, & Kashian 2013), although competition could lead to their extirpation in dense conifer stands (Kaye, Stohlgren, & Binkley 2003). By

resprouting, however, aspen may benefit from a critical mechanism of persistence, should a fire reburn stands. Our sample size of excavated aspen was small due to logistical constraints, however, root development over the last 25 years suggests that Yellowstone's postfire aspen may have sufficient lateral roots to resprout after fire. Resprouting aspen can grow faster than seedling conifers and can even dominate early postfire succession (Schier & Campbell 1978; Bartos, Brown, & Gordan 1994; Frey et al. 2003; Johnstone & Chapin 2006b). In Yellowstone, the 2000 Boundary Fire re-burned 12-year old lodgepole pines and seedling aspen that regenerated after the 1988 fires. Young pines had not developed a seedbank before reburning. Thirteen years after the Boundary Fire, we observed that aspen density was five times greater than lodgepole pine density, and many aspen were more than two meters tall (Turner et al. Unpublished data).

Our long-term study of a 25-year old colonizing aspen cohort suggests a shifting landscape mosaic where ecological filters that facilitate or constrain colonizing species vary in space and time. Many of the filters change slowly, and thus, it is difficult to anticipate where on the landscape a colonizing species will succeed without ongoing measurement of the organisms and their local environment. Our findings underscore the need for long-term study and the value of tracking colonizing cohorts for rigorously characterizing population responses to 21<sup>st</sup> century environmental change.

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## Tables

**Table 1.** (A) Logistic regression results from top models (AICc < 2) predicting aspen presence in 1999 and persistence to 2012 if aspen were present in 1999. Coefficients (SE) are presented. (B) Linear regression results from top models (AICc < 2) predicting aspen density in 1999 and if aspen persisted from 1999 to 2012. Coefficients (SE) are presented. Model fit includes likelihood ratio tests for logistic regressions and Adj. R<sup>2</sup> for linear models.

	<i>Climate</i>		<i>Topo-edaphic conditions</i>				<i>Conifer competition</i>		Model
	Log	Log					Log		
	Growing season	Annual					Rhyolite	Lodgepole	
	Intercept	temperature	precipitation	Elevation	Rhyolite till	Rhyolite glacial	low base	pine ANPP	Fit
<b>A.</b>									
<i>1999 aspen presence</i>									
Model 1	-25.98**	30.04 (14.86)**			-0.34 (1.36)	-3.96 (1.46)***	-0.65 (0.78)	5.33 (1.97)***	32.0***
Model 2	-2.75		8.74 (4.37)**	-0.01 (0.004) **	-0.67 (1.39)	-4.66 (1.63)***	-0.90 (0.78)	6.40 (2.26)***	33.8***
Model 3	-35.28**	28.44 (15.19)*	3.59 (3.65)		-0.39 (1.36)	-4.09 (1.52)***	-0.65 (0.77)	6.13 (2.19)***	33.0***
<i>2012 aspen persistence</i>									
Model 1	-8.61*			0.004 (0.002)*					3.2*
Model 2	18.71*	-19.64 (12.04)*							2.8*

Model 3	0.31				-
Model 4	7.64	-20.62 (12.27)*	4.13 (4.55)		3.7
Model 5	3.15	-9.53 (16.8)		0.003 (0.003)	3.54

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**B.**

*1999 aspen density*

Model 1	-5.02*	8.17 (2.89)***			0.14
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*2012 aspen density*

Model 1	2.17***				-
Model 2	2.66	5.19 (3.45)			0.05
Model 3	2.42***			-0.35 (0.26)	0.03
Model 4	-1.55		1.27 (0.98)		0.03
Model 5	-9.12	8.84 (4.23)**		0.001 (0.001)	0.08
Model 6	-2.29	5.05 (3.39)		-0.34 (0.26)	0.08

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\*P≤0.1, \*\*P<0.05, \*\*\*P<0.01

**Table 2.** (A) Linear regression results from top models (AICc < 2) predicting mean aspen height in 1996, 2000 and 2013. (B) Linear regression results from top models (AICc < 2) predicting mean aspen basal diameter in 1996, 2000 and 2013 at 21 aspen size plots. Coefficients are presented (SE). Data from 1996 and 2000 have been previously published in Romme et al. 2005.

							<i>conifer</i>
		<i>Climate</i>		<i>Topo-edaphic conditions</i>		<i>competition</i>	
	Growing season	Annual		Log	Log lodgepole	Adj.	
	Intercept	temp	precipitation	Soil pH	total soil N	pine density	R <sup>2</sup>
<b>A.</b>							
<i>1996 height</i>							
Model 1	0.01			0.22 (0.07)***	-0.24 (0.11)**		0.38
<i>2000 height</i>							
Model 1	-0.38			0.33 (0.08)***			0.43
Model 2	-0.01			0.31 (0.08)***		-0.07 (0.05)	0.46
Model 3	-0.80		0.0004 (0.0003)	0.34 (0.08)***			0.44
Model 4	-0.28			0.33 (0.08)***	0.12 (0.12)		0.43
<i>2013 height</i>							
Model 1	-0.16			0.47 (0.12)***	0.62 (0.19)***		0.48
Model 2	0.36			0.44 (0.12)***	0.64 (0.19)***	-0.09 (0.06)	0.52

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**B.***1996 Basal diameter*

Model 1	-0.08			0.16 (0.09)*		0.10
Model 2	-0.98	0.23 (0.13)*				0.10
Model 3	0.84***					
Model 4	1.34***		-0.001 (0.0004)			0.08
Model 5	0.46		-0.001 (0.0004)	0.15 (0.09)		0.15
Model 6	-0.29	0.10 (0.15)	-0.0004 (0.0005)	0.12 (0.10)		0.12

*2000 Basal diameter*

Model 1	-1.40	0.30 (0.11)**				0.24
Model 2	-1.47	0.21 (0.12)*		0.14 (0.09)		0.30
Model 3	-0.23			0.21 (0.08)**		0.23
Model 4	-0.39			0.21 (0.08)**	-0.18 (0.11)	0.28
Model 5	-1.02	0.29 (0.11)**			-0.07 (0.05)	0.28
Model 6	-0.03			0.20 (0.07)**	-0.19 (0.11)*	0.33
Model 7	0.10			0.20 (0.08)**		0.25
Model 8	-1.12	0.21 (0.12)*		0.13 (0.08)	-0.06 (0.05)	0.33

*2013 Basal diameter*

Model 1	-0.23			0.36 (0.10)***	0.32 (0.15)**	-0.10 (0.05)**	0.50
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Model 2	-0.39	0.32 (0.10)***	-0.09 (0.05)*	0.40
Model 3	-0.83	0.39 (0.10)***	0.30 (0.16)*	0.39

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\*P<0.1, \*\*P<0.05, \*\*\*P<0.01



**Table 3.** Measurements of 10 excavated aspen and lodgepole-pine stand characteristics at six sites. Height and basal diameter measurements of ramets are calculated only for aspen that produced ramets. Biomass measurements exclude one site because not all belowground biomass could be harvested, due to logistical constraints.

	Mean	SE	Median	Min.	Max.	Obs.
<i>Dominant stem morphology</i>						
Dominant stem height (cm)	117.3	25.0	91.5	40.0	300.0	10
Dominant stem basal diameter (cm)	2.4	0.6	2	1.1	7.6	10
Age in 2014	19.2	1.1	20	12	24	10
<i>Ramet morphology</i>						
Number of ramets	1.6	0.7	1	0	7	10
Ramet height (cm)	49.7	10.8	32.5	7.5	135.0	16
Ramet basal diameter (cm)	1.4	0.4	0.7	0.3	4.5	16
<i>Root morphology</i>						
Number of lateral roots	5.2	0.77	4.5	2	10	10
Lateral root length (cm)	166.1	30.2	101.5	16.5	973.0	10
<i>Live biomass</i>						
Aboveground woody biomass (g)	698.6	625.5	66.9	34.0	5,700.9	9
Leaf biomass (g)	54.3	44.6	6.9	1.63	430.3	9
Belowground biomass (g)	374.0	331.4	35.0	25.0	3,025	9
<i>Ratios</i>						
Above:Belowground biomass ratio	1.7	0.2	1.9	0.8	2.8	9
Root: whole plant biomass ratio	0.4	0.03	0.3	0.2	0.5	9
Dominant stem height: median root length	1.0	0.18	1.0	0.3	2.2	10
Dominant stem height: mean root length	1.0	0.18	1.0	0.3	2.2	10
Dominant stem height: max root length	0.7	0.16	0.6	0.23	1.9	10

Total stem height: total root length	0.33	0.09	0.23	0.13	1.1	10
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**Table 4.** Summary of trends in ecological filters between 1996-2000 and 2013 and their shifting influence on the presence, persistence, and size of a colonizing postfire aspen-seedling cohort in Yellowstone National Park

Filter	1996-2000 (8-12 years postfire)	Filter trend 1996-2013	2012-2013 (24-25 years postfire)
Growing season temperature	<b>Strong filter:</b> Cold temperatures precluded aspen presence at high elevations but permitted presence at warmer lower elevations.	<b>Increase.</b> Substantial warming (7.7°C to 8.5°C from 1990s to 2000s).	<b>Strong filter:</b> Aspen persisted at mid-elevations with cooler temperatures but were eliminated at lower-warmer elevations.
Lodgepole pine competition	<b>No filter:</b> Lodgepole pine seedlings too small to compete with aspen seedlings.	<b>Increase.</b> Rapid growth of lodgepole pine.	<b>Strong filter:</b> Smaller aspen with high lodgepole pine density.
Soil nitrogen	<b>Weak filter:</b> Shorter aspen in plots with high total soil N.	<b>Decrease.</b> Decline in total soil N, particularly where total soil N had been high in 1996-2000.	<b>Strong filter:</b> Taller aspen with greater total soil N.
Ungulate browsing	<b>Strong filter:</b> Uniformly heavy browsing (~90% of stems browsed) kept stems short.	<b>Decrease.</b> Substantial decline in elk density and browsing.	<b>No filter:</b> Aspen size no longer influenced by browsing (< 3% of stems browsed).

Soil pH

**Strong filter:** Larger stems in  
more basic soils.

**No change.**

**Strong filter:** Larger stems in  
more basic soils.

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### Figure Captions

**Figure 1.** Map of the study plots across the central plateau, Yellowstone National Park, WY, USA. Blue circles are 72 aspen presence and density plots sampled in 1999 (11 years postfire) and 2012 (24 years postfire). Red dots are 21 aspen size plots sampled in 1996 (8 years postfire), 2000 (12 years postfire), and 2013 (25 years postfire). Black squares are six aspen excavation plots sampled in 2014 (26 years postfire).

**Figure 2.** Aspen seedling presence in 1999 and persistence from 1999 to 2012 vs. growing season temperature ( $^{\circ}\text{C}$ ), elevation (m), and lodgepole pine ANPP ( $\text{Mg ha}^{-1} \text{yr}^{-1}$ ).

**Figure 3.** Mean aspen (A.) height (cm) and (B.) basal diameter (mm) in 1996 ( $n=392$ ), 2000 ( $n=392$ ), and 2013 ( $n=381$ ) at 21 aspen size plots. Values are mean  $\pm$  one standard error. Data from 1996 and 2000 have been previously published in Romme et al. 2005.

**Figure 4.** Mean aspen height (cm) and basal diameter (mm) in 1996, 2000, and 2013 vs. total soil N (%), and log transformed lodgepole pine density ( $\text{ha}^{-1}$ ). Data from 1996 and 2000 have been previously published in Romme et al. 2005.

**Figure 5.** Stem height to lateral root length ratios vs. lodgepole pine density ( $\text{ha}^{-1}$ ) for 10 excavated aspen in 2014 (26 years postfire) (Kendall's Tau= 0.44 - 0.58,  $P < 0.10$ ).

## Figures

Figure 1.

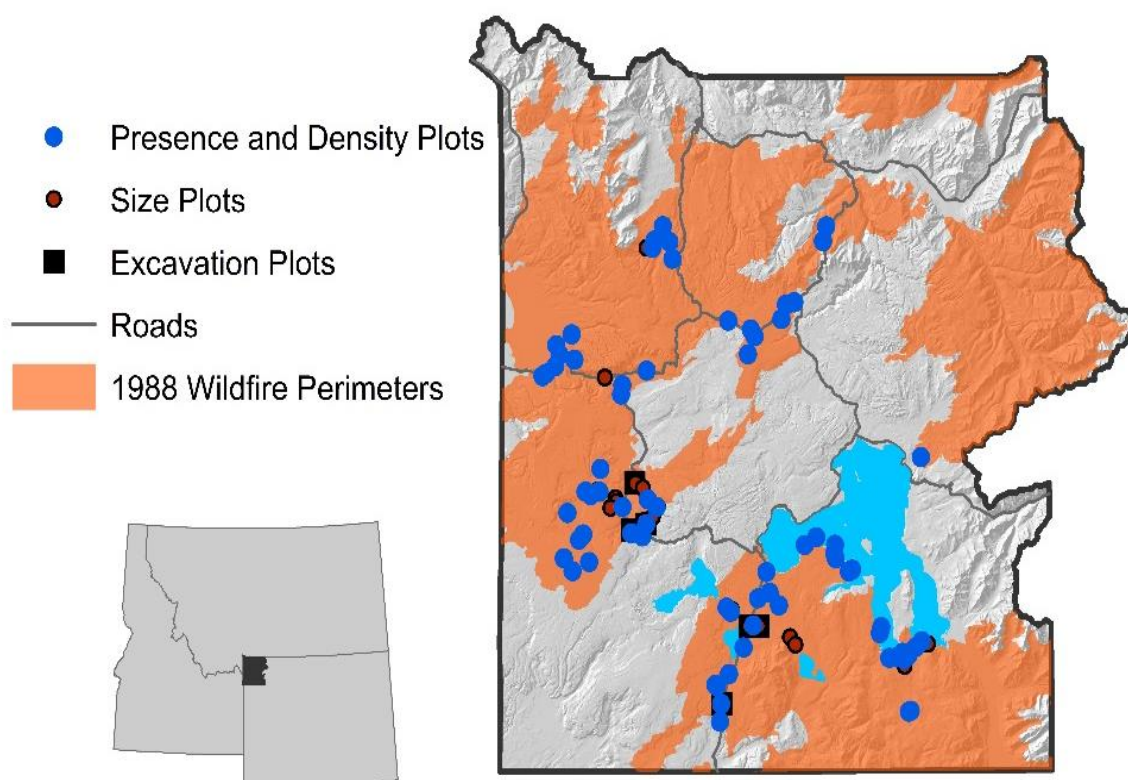


Figure 2.

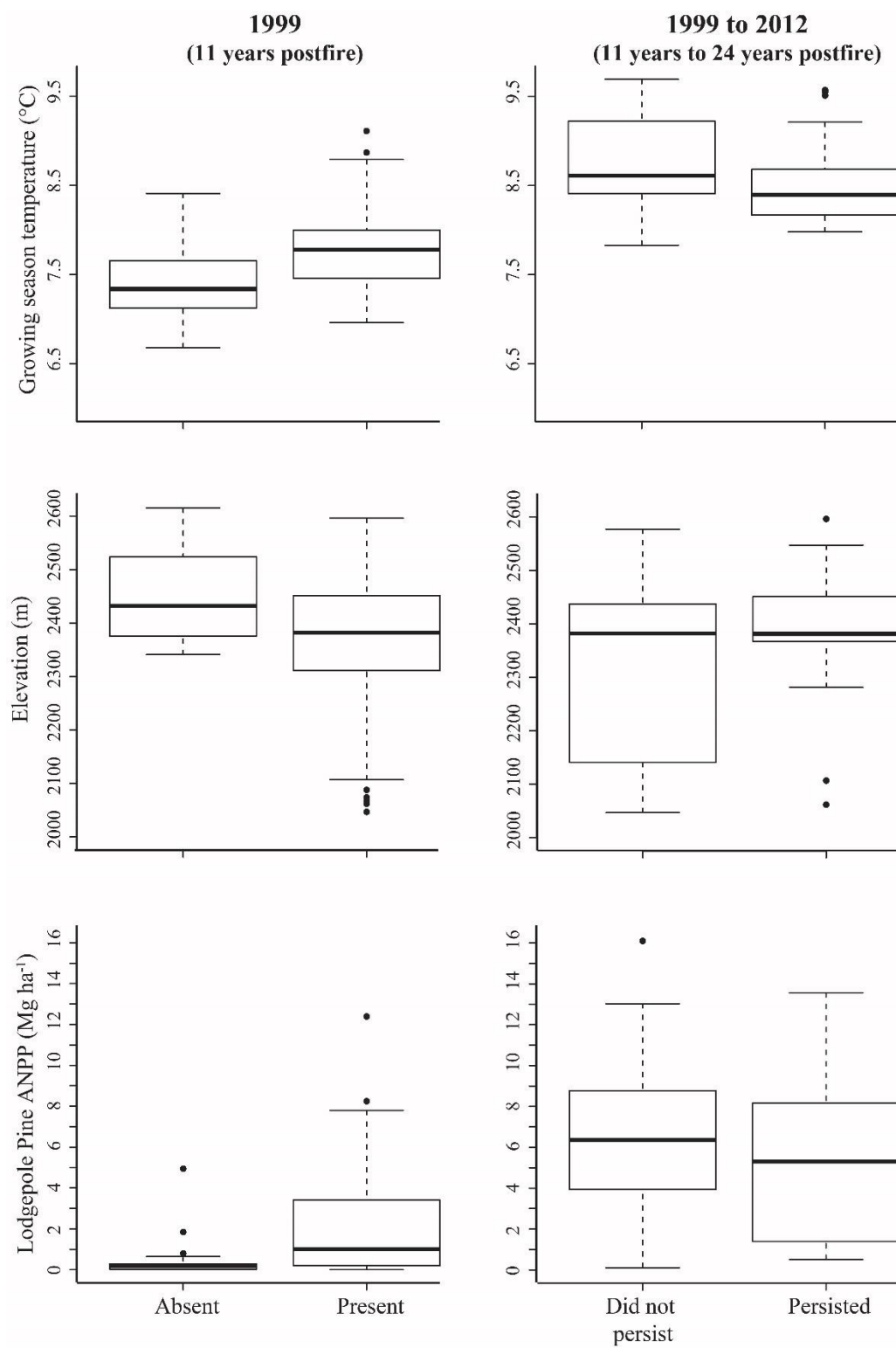


Figure 3.

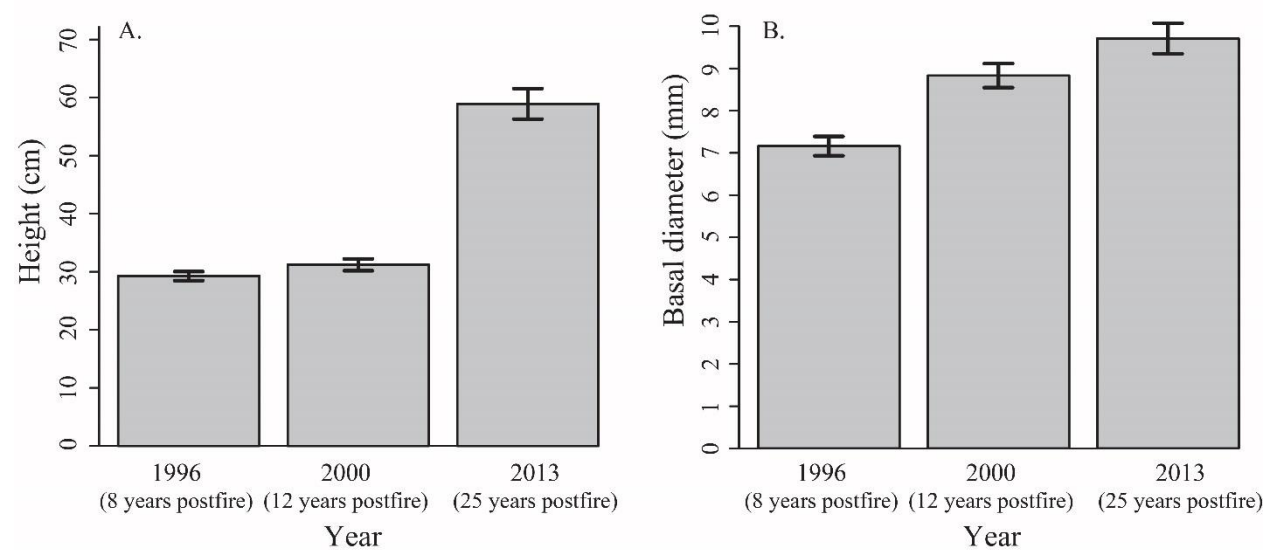




Figure 4.

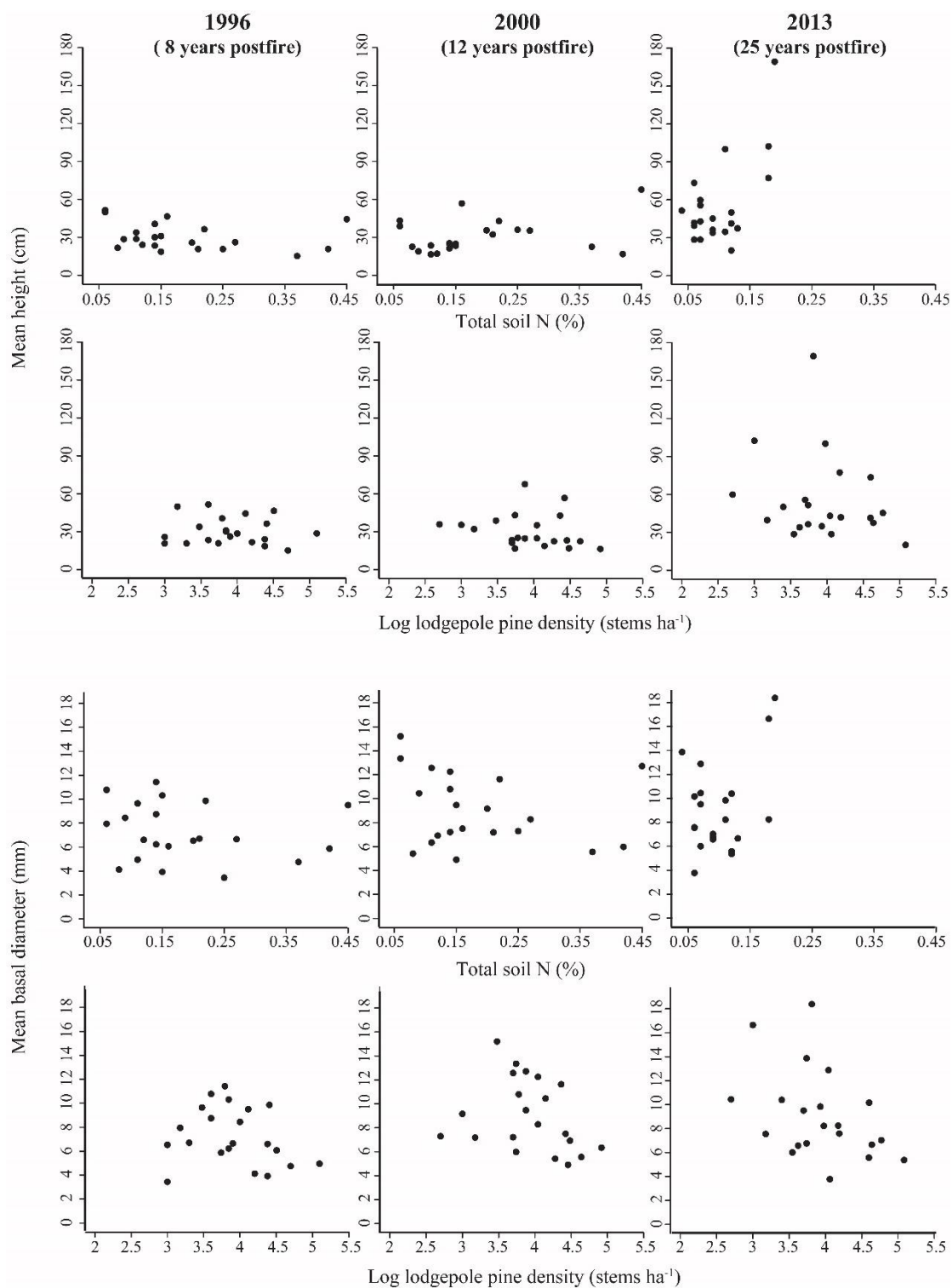
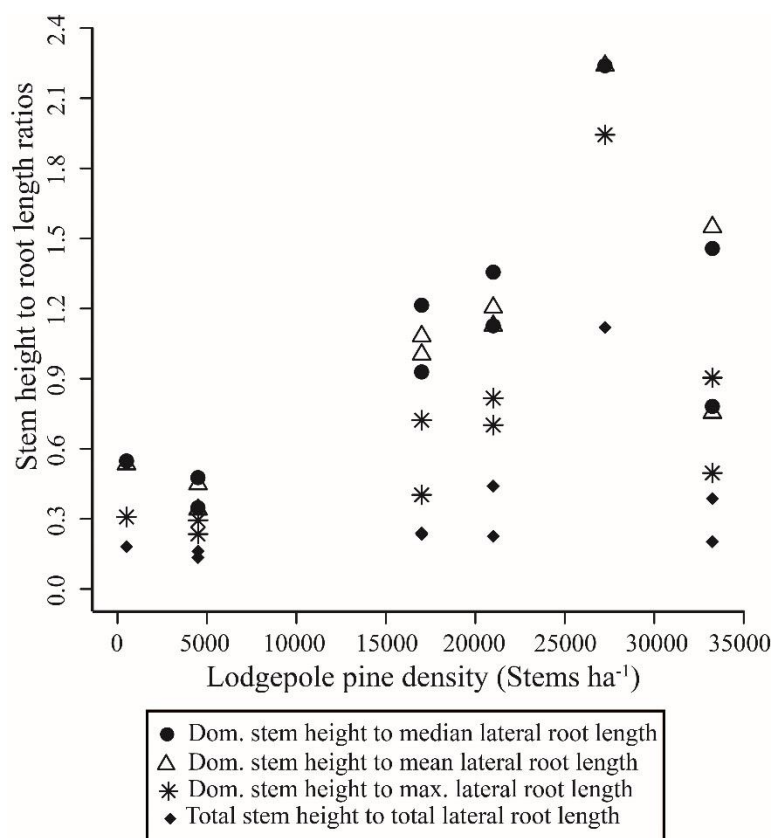


Figure 5.



## Supplemental Material

### Appendix A

Descriptive statistics of predictor variables used in analyses of postfire aspen presence and density in 1999 and 2012 ( $n = 72$  plots). Values are mean (SE) (Min–Max).

Predictor variables	1999	Both years	2012
<i>Climate</i>			
Growing season temp (°C)	7.7 (0.1)		8.5 (0.1)
	(6.7–9.1)		(7.8–9.7)
Annual precip. (mm yr <sup>-1</sup> )	881.6 (23.3)		829.7 (22.2)
	(618.8–1542)		(586–1479.4)
<i>Topo-edaphic</i>			
Elevation (m)		2,392.2 (16.4)	
		(2,047– 2,615)	
Rhyolite till (0,1)		0.08 (0.03)	
		(0–1)	
Rhyolite glacial (0,1)		0.13 (0.04)	
		(0–1)	
Rhyolite low base sat. (0,1)		0.61 (0.06)	
		(0–1)	
Andesite (0,1)		0.18 (0.05)	
		(0–1)	
<i>Conifer competition</i>			
Lodgepole ANPP (Mg ha <sup>-1</sup> yr <sup>-1</sup> )	1.5 (0.3)		5.0 (0.5)
	(0–12.4)		(0–16.5)

## Appendix B

Descriptive statistics of predictor variables used in analysis of postfire aspen height and basal diameter in 1996, 2000, and 2013 ( $n = 21$  plots). Values are mean (SE) (Min–Max).

Predictor Variables	1996	2000	2013
<i>Climate</i>			
Growing season temp (°C)	8.0 (0.06)	7.7 (0.06)	8.4 (0.03)
	(7.3–8.2)	(7.2–8.0)	(8.1–8.7)
Annual precip (mm yr <sup>-1</sup> )	750.3 (17.3)	830.0 (19.5)	780.4 (17.4)
	(662.6–877.4)	(734.7–977.8)	(694.6–911.1)
<i>Topo-edaphic</i>			
Total soil N (%)	0.2 (0.02)	0.2 (0.02)	0.1 (0.01)
	(0.06–0.5)	(0.06–0.5)	(0.04–0.2)
Soil pH	5.6 (0.1)	5.6 (0.1)	5.3 (0.06)
	(4.7–6.3)	(4.7–6.3)	(4.9–6.1)
<i>Conifer competition</i>			
Lodgepole pine density (stems ha <sup>-1</sup> )	17,605 (6,025)	16,071 (4,174)	19,543 (6,237)
	(1,000–125,000)	(500–82,500)	(500–121,500)

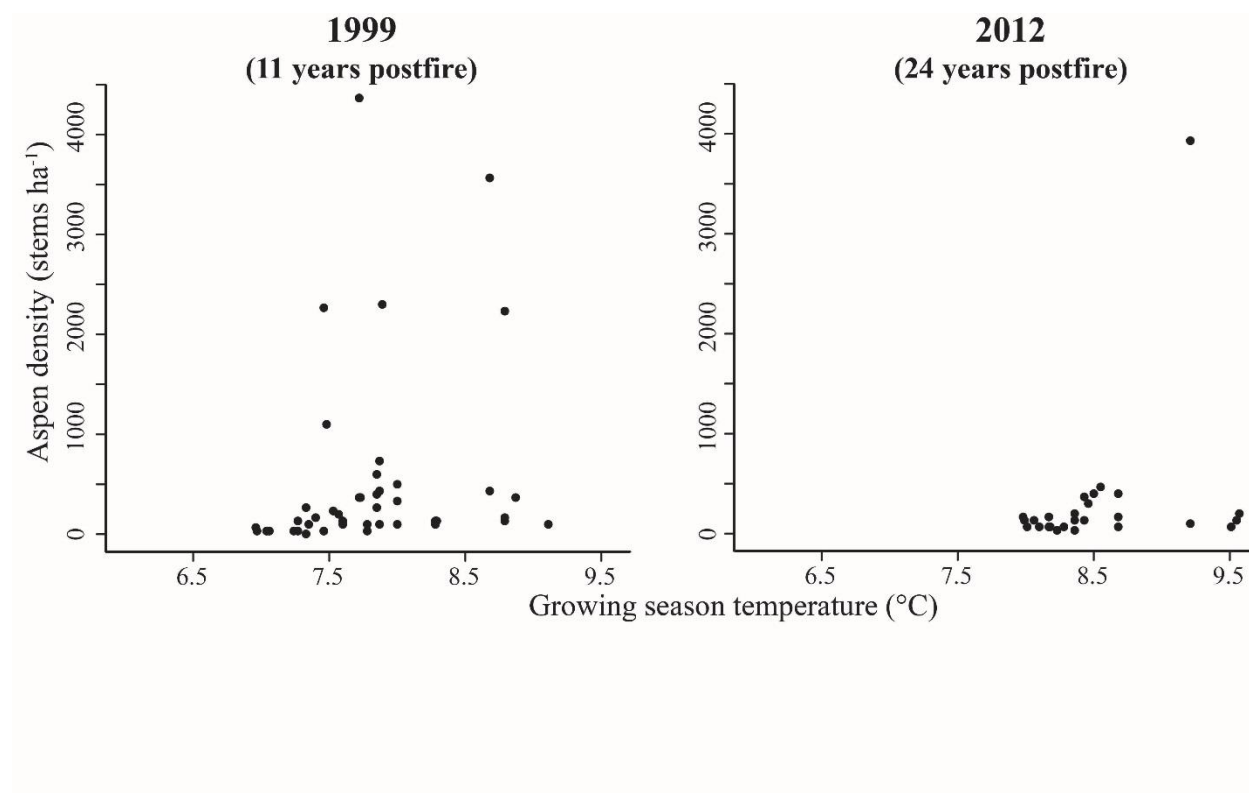
## Appendix C

Factor analysis of 1996 soil variables showing rotated factor patterns.

Variables	Factor 1	Factor 2
Total soil nitrogen	0.97	0.24
% Soil organic matter	0.93	0.42
Soil pH	-0.11	0.51
Available soil phosphorous	0.06	0.42

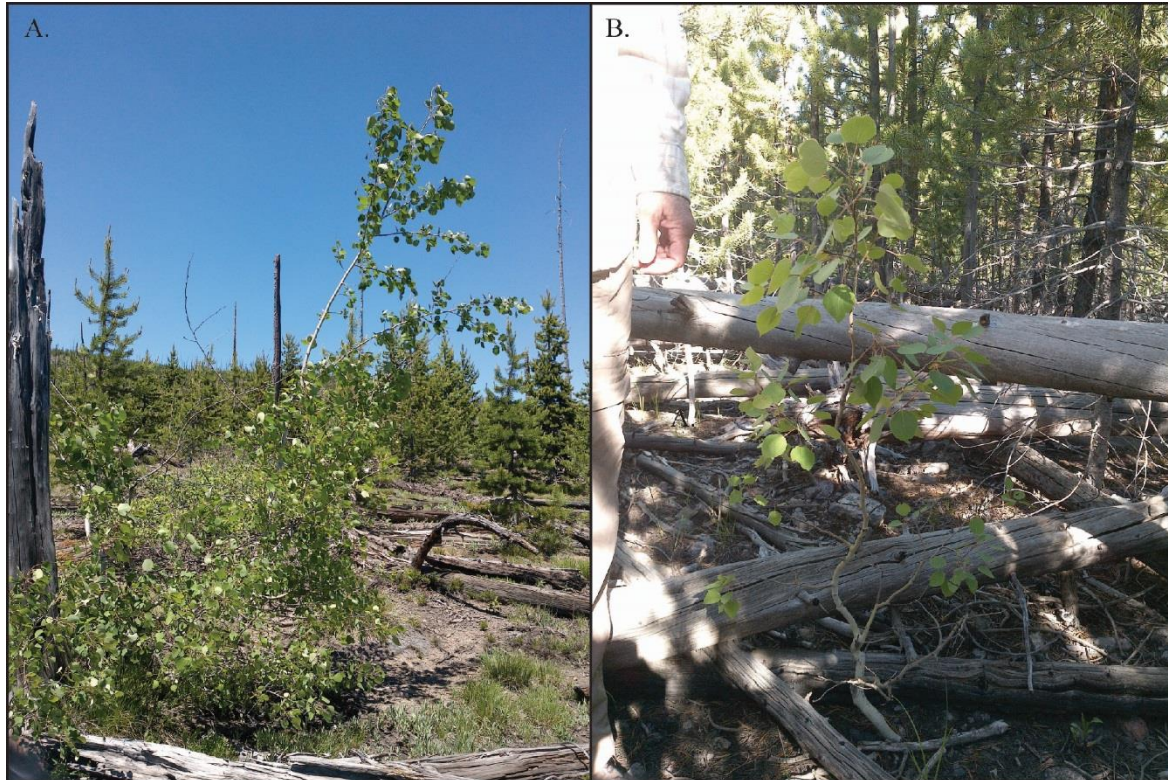
## Appendix D

Aspen seedling densities in 1999 and 2012, where aspen were present, vs. growing season temperature ( $^{\circ}\text{C}$ ).



## Appendix E

Postfire aspen grow very slowly on the central plateau of Yellowstone National Park, WY, USA. After 25 years, the tallest surveyed aspen (A.) was just over three m tall. Mean aspen size was approximately 0.6 m tall (B.).



**Chapter 2 – Origins of abrupt change? Postfire subalpine conifer regeneration declines  
nonlinearly with warming and drying**

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## ABSTRACT

Twenty-first century warming and drying could initiate abrupt change in subalpine forests if postfire temperature and soil-moisture conditions become less suitable for tree seedling establishment. Using two widespread conifer species, lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), we conducted complementary experiments to ask: (1) How will projected early- to mid-21<sup>st</sup> century warming and drying in Yellowstone National Park (Wyoming, USA) affect postfire tree seedling establishment and mortality? (2) How do morphological traits of tree seedlings differ between species and vary with climate and soil? With a four-year *in situ* seed-planting experiment and a shorter-term (one growing season) controlled-environment experiment, we identified how combinations of climate (historical, early-21<sup>st</sup> century, mid-21<sup>st</sup> century) and soil type (infertile volcanic derived, less infertile sedimentary derived) influence tree seedling establishment, growth, and survival. In our field experiment, an increase of just 2°C in median daily soil surface temperatures (from 15.1°C to 17.1°C) and a five-percentage point decrease (from 16.9% to 11.8%) in median daily soil moisture led to 92% and 76% reduction in establishment of lodgepole pine and Douglas-fir, respectively, and 100% seedling mortality after three growing seasons. Thus, thresholds associated with nonlinear changes in postfire tree-seedling establishment were ~16°C for growing season temperature and ~15% for soil moisture. Seedling establishment and mortality also varied with aspect; approximately 1.7 times more seedlings established on mesic versus xeric aspects, and fewer seedlings died. In the controlled-environment experiment, warming led to increased tree seedling establishment, as might be expected at upper treeline or higher latitudes. Soil type was also important. Three times more seedlings established on volcanic-

derived soils than on sedimentary-derived soils, which had poor water holding capacity. Seedling morphology differed between species. Lodgepole pine grew taller than Douglas-fir and produced more needles under mid-21<sup>st</sup> century conditions. Douglas-fir had larger root-to-shoot length ratios than lodgepole pine, and the difference between species increased with drying. Projected warming and drying in Yellowstone appear likely to exert powerful influence on postfire tree regeneration, which could underpin fundamental change in subalpine forest structure and tree-species composition.

**Key words:** *Climate change; Drought; Forest resilience; Seedling establishment; Seedling morphology; Soil; Succession; Wildfire; Yellowstone National Park*

## INTRODUCTION

Concern is growing among ecologists that forests may change profoundly over the next few decades as temperatures warm and natural disturbances increase in frequency and severity (Gauthier et al. 2015, Trumbore et al. 2015, Ghazoul and Chazdon 2017). Climate and disturbance regimes with no analogue during the past 10,000 years are projected for many places in the 21<sup>st</sup> century (Westerling et al. 2011, Kelly et al. 2013). Resilience is the capacity of a system to absorb disturbances while retaining function, structure, feedbacks, and thus identity (Walker et al. 2006). Whether forests will remain resilient to changing conditions or instead transition to fundamentally different ecosystem states remains unresolved (Ghazoul et al. 2015, Reyer et al. 2015, Johnstone et al. 2016).

There is tremendous interest in determining how and why regional forests may change in the 21<sup>st</sup> century because consequences for carbon storage (Bonan 2008, Seidl et al. 2014), climate regulation (Thom et al. 2017a), biodiversity (Thom et al. 2017b), and provision of ecosystem services (Turner et al. 2013, Seidl et al. 2016) may be profound. However, changes in regional forests are likely to emerge from the aggregate effects of drivers that act on local processes, such as reproduction, seedling establishment, tree growth, and mortality (Allen and Starr 1982, Filotas et al. 2014, Rose et al. 2017). Just like a mosaic where the image consists of many smaller interwoven pieces, regional-forest identities are a property of their components (Messier et al. 2015). Thus, research identifying and characterizing the fine-scale mechanisms underpinning regional forest responses to changing climate and disturbance is essential.

Erosion of ecosystem resilience and transitions to alternate states generally require two steps (Petraities and Latham 1999). First, an origin mechanism, or an ecosystem process capable

of producing fundamental change, must initiate transition to an alternate state (Jackson 2006), then positive feedbacks must stabilize that alternate state (Connell and Slatyer 1976, Connell and Sousa 1983). Identifying origin mechanisms is critical, as positive feedbacks are irrelevant if transitions are not first initiated. In forests, there are often lagged responses to origin mechanisms because mature trees are long lived and tolerate a wide range of environmental conditions. Thus, the origins of change in forests are often difficult to identify (Lloret et al. 2012). However, large severe disturbances can catalyze more rapid reorganization (Crausbay et al. 2017). In the Alaskan boreal forest, for example, increased severity of large stand replacing fires (i.e., where all trees are killed) has caused regional transitions in postfire tree-species composition from spruce to deciduous dominance (Mann et al. 2012).

In subalpine forests of western North America, stand replacing fires have historically been part of an adaptive cycle (Romme 1982, Turner et al. 1994, Holling 2001, Johnstone et al. 2004, Allen et al. 2014) (Fig. 1A). Forests burn, creating a seed bed, freeing up previously-stored nutrients (Turner et al. 2007), and increasing light availability for seedling establishment. Tree establishment during the first few years postfire sets the template that shapes stand structure and tree-species composition for decades to centuries (Turner et al. 1997, 2004, Kashian et al. 2005). Tree seedlings are very sensitive to temperature and soil moisture (Lotan 1964, Cochran and Berntsen 1973, Rochefort et al. 1994, Walck et al. 2011, Kueppers et al. 2017), however, and warmer-drier conditions following fires could initiate abrupt change in subalpine forests as conditions become less suitable for tree regeneration (Johnstone et al. 2010, Landhäusser et al. 2010, Liang et al. 2017) (Fig. 1B, 1C).

If tree seedlings establish, inter- and intra-specific variation in plant traits play an important role in determining which individuals survive and thrive (Richter et al. 2012) (Fig. 1D). For example, in response to experimental drought treatments in subalpine forests of Colorado, limber pine (*Pinus flexilis*) seedlings grew longer roots, allowing them to better capture water in drying soil than seedlings of other tree species (Lazarus et al. 2018). Differences in plant traits among species are often consistent with broader life history strategies (e.g, limber pine trees are drought tolerant) and generally involve tradeoffs (e.g., prioritizing belowground growth over aboveground growth) that may confer advantage to some environmental conditions, while disadvantaging seedlings in other conditions (Eskelinen and Harrison 2015). Individuals of the same species also display trait plasticity, or the ability of a genotype to modify phenotypic expression in response to environmental conditions (Berg and Ellers 2010). In fact, intraspecific variation of traits can sometimes be greater than interspecific variation (Malyshev et al. 2016). Seedling traits will likely mediate climate change effects on competitive interactions (Kunstler et al. 2016), individual growth and survival (Soudzilovskaia et al. 2013), successional trajectories, and tree-species distributions (Salguero-Gómez et al. 2016).

Experiments are a valuable tool for understanding how postfire tree regeneration may respond to climate change because they are designed to reveal mechanisms and attribute causation (Carpenter 1998, Thompson et al. 2014, Nooten and Hughes 2017). In contrast, field observations often lack sufficient controls, and can be difficult to replicate, particularly when studying phenomena that rarely occur (Jentsch et al. 2007). Experiments are also useful for finding thresholds where incremental changes in environmental drivers cause nonlinear system responses (Groffman et al. 2006, Kreyling et al. 2013). Designing climate change experiments is

not always straightforward, however, because multiple climate variables are projected to change simultaneously, making them difficult to untangle (Kreyling and Beier 2013, De Boeck et al. 2015). Further, there are inherent tradeoffs in experimental design between treatment realism and controlling for other abiotic and biotic factors that also influence tree regeneration. Finally, climate change effects can take years to manifest (Tilman 1989) and can play out over large spatial domains (Petraitis and Latham 1999). Here, we present two experiments that were designed with these challenges in mind. The experiments encompass both *in situ* and controlled conditions and explore the multi-year effects of projected 21<sup>st</sup> century warming and drying on postfire regeneration of two widespread subalpine conifers, lodgepole pine (*Pinus contorta* var. *latifolia*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) in Yellowstone National Park (Wyoming, USA).

Yellowstone is an excellent place to study how changing climate may alter postfire tree regeneration. The park is primarily a large central subalpine plateau, mostly underlain by very infertile soils derived from volcanic rhyolite parent material (Despain 1990). Subalpine forests are dominated by lodgepole pine and have experienced large stand-replacing fires at 100- to 300-year intervals throughout the Holocene (Romme et al. 1982, Millspaugh et al. 2000, Power et al. 2011). Lodgepole pine is well adapted to regenerate prolifically after large fires (Turner et al. 1997b). Historically, postfire regeneration has been robust, and tree growth during early succession has been rapid (Turner et al. 2004, 2016). Lower montane forests of Yellowstone are composed of drought tolerant Douglas-fir trees, which regenerate more slowly after fire (Donato et al. 2016) and trade rapid aboveground growth for investment in deep root systems (Burns and Honkala 1990). Evidence suggests Douglas-fir trees cannot tolerate the rhyolite-derived soils

found on the central plateau (Despain 1990, Whitlock 1993). In the 21<sup>st</sup> century, warming and drying conditions are projected (Westerling et al. 2011) that may be incompatible with continued postfire establishment of either species within their current distributions (Hansen and Phillips 2015).

We conducted two complementary seed planting experiments, a four-year *in situ* soil transplant experiment in Yellowstone and a shorter (one growing season) controlled-environment experiment to ask: (1) How will projected early- to mid-21<sup>st</sup> century warming and drying in Yellowstone National Park affect postfire tree seedling establishment and mortality? We hypothesized that lodgepole pine seedlings currently experience soil moisture conditions at the edge of their drought tolerance, so projected warming and drying would reduce postfire lodgepole pine seedling establishment. We also expected that warming would enhance establishment of Douglas-fir seedlings, but only on more fertile soils than those derived from rhyolite. We expected that neither species would establish on rhyolite-derived soils under future climate conditions. If seedlings establish, differences in morphological traits among seedlings could confer advantage under warming and drying conditions. Therefore, we asked: (2) How do morphological traits differ between species and vary with climate and soil? In response to warming, given sufficient water, we expected lodgepole pine to grow taller and produce more needles. In response to drying, we expected Douglas-fir to grow longer roots.

## STUDY AREA AND METHODS

### *Study area*

Yellowstone National Park (Fig. 2A) spans ~ 9,000 km<sup>2</sup> at the corners of Wyoming, Idaho, and Montana. Elevation in Yellowstone ranges from 1,600 m to 3,400 m, with lower tree

line at 1,800 m and upper tree line at 3,050 m (Despain 1990). At low elevations current climate is relatively warm and dry with a mean July temperature of 17.5 °C and 390 mm of annual precipitation (Western Regional Climate Center 2017). Sagebrush grasslands transition to Douglas-fir forests, with some pockets of trembling aspen (*Populus tremuloides*), at lower treeline (Romme et al. 1995). Stand densities in Douglas-fir forests are strongly determined by aspect; more dense stands are found on north facing mesic slopes and sparse, park-like stands occupy dry south facing slopes (Donato et al. 2016). Climate is cooler and wetter on the central subalpine plateau, with a mean July temperature of 14 °C and annual precipitation of 584 mm, most of which falls as snow during the winter (Western Regional Climate Center 2017). Lodgepole pine trees dominate forests on the plateau. Early postfire (< 30-yr old) densities of lodgepole pine forests vary widely (0 - 555,000 stems ha<sup>-1</sup>) (Turner et al. 2004), which is primarily determined by the level of prefire serotiny and fire severity (Turner et al. 1999).

Soils on the central plateau are derived from a volcanic rhyolite parent material, with some pockets derived from older volcanic andesite or sedimentary materials (Despain 1990). Rhyolite-derived soils contain half the total nitrogen (N) of andesite-derived soils (Despain 1990). Rhyolite soils also have lower clay content, and thus, lower cation exchange and water holding capacities (Despain 1990). Spring and summer temperatures in Yellowstone are projected to warm by 4.5 to 5.5 °C near the end of the 21<sup>st</sup> century, which could both increase fire activity substantially (Westerling et al. 2011) and change the environmental context of postfire tree establishment. Trends in climate and fire may be incompatible with current tree-species composition and forest structure during the 21<sup>st</sup> century (Piekielek et al. 2015, Clark et al. 2017, Loehman et al. 2017).



### *Field experimental design*

To test effects of warm-dry conditions and soil type on postfire lodgepole pine and Douglas-fir regeneration, we conducted an *in situ* experiment in Yellowstone between August 2014 and August 2017 (Fig. 2). The experiment was a 2 x 2 factorial design of two climate treatments and two soil types. Climate treatments included current conditions in subalpine forests of Yellowstone and warmer-drier conditions consistent with projected mid-21<sup>st</sup> century climate in subalpine forests of Yellowstone. Because no recent fires had burned on andesite-derived soils, the experiment included either soils derived from rhyolite or soils from sedimentary parent material, which are also considered more fertile than rhyolite.

To select experimental sites, we used gridded climate projections (12-km resolution) of moisture deficit (annual precipitation minus annual potential evapotranspiration) from the 4<sup>th</sup> International Panel on Climate Change report (IPCC 2007), made available by the Nature Conservancy's Climate Wizard database (<http://climatewizard.org/>). We selected an ensemble product of three general circulation models (GCMs) that accurately represent historical conditions in Yellowstone, CCSM 3.0, CNRM CM3.0, and GFDL CM 2.1 (Westerling et al. 2011) forced with the A1B (middle of the road) emissions scenario. Using the ensemble, we first characterized the mean growing season moisture deficit and its standard deviation between 2050 and 2060 for pixels within the current distribution of lodgepole pine in Yellowstone. We then identified pixels in Yellowstone where recent (2002-2012) growing season moisture deficit was consistent with the future projections of moisture deficit that we calculated for lodgepole pine forests (Fig. 2B). These pixels fell at lower tree line in sagebrush grassland (elevation ~ 2,000 m) and we selected three experimental sites within these pixels to be our warm-dry treatment (Fig.

2A). We located our high-elevation cool-wet experimental sites in lodgepole pine forest (elevation = ~ 2,430 m) that had recently burned in stand replacing fires (between 2008 and 2012) (Fig. 2A). At each site, we installed one set of experimental plots in 2014 and another set in 2015, separated by > 100 m.

In the summers of 2014 and 2015, intact soil cores were collected ( $n = 168$  each summer, 336 total) from two recent fires (both burned in 2012). Soil cores derived from rhyolite parent material were collected from the Cygnet Fire (1,400 ha), which burned lodgepole pine-dominated subalpine forest in Yellowstone National Park. Soil cores derived from sedimentary parent material were collected from the Fontanelle Fire (19,000 ha) in the southern Greater Yellowstone Ecosystem. Both fires were severe and stand replacing (i.e., all understory vegetation and overstory canopy was killed). Lodgepole pine was present before the Cygnet Fire and both lodgepole pine and Douglas-fir were present before the Fontanelle Fire. Flat soil collection sites were chosen within each fire perimeter to minimize any aspect or topographic effects. At each soil collection site, two 50-m transects were established in a north to south direction and a soil core (10-cm diameter by 20-cm depth) was harvested on each side of the transect using PVC tubes at ~ 1-m increments. Soil samples (10-cm depth) were also collected, sieved, and dried at 60 °C for 24 hours, and then were analyzed for soil texture (% sand, % silt, % clay), % total soil N (micro Kjeldhal procedure), soil pH (measured in water), % organic matter (determined using dry combustion), and available phosphorous (Bray P1 extract) by the University of Wisconsin Soil and Plant Analysis Laboratory, Madison, WI, USA (UW SPAL 2013). Soil cores were kept cool during transport and storage.

At each study site, one experimental plot was established in 2014 and 2015. In each experimental plot, 14 cores of rhyolite and 14 cores of sedimentary-derived soils ( $n=28$  total) were planted in clusters of four cores, with each cluster separated by 50 m (Fig. 2C). Experimental plots were arranged in a hexagon with six clusters of soil cores on the outside surrounding a middle cluster (Fig. 2C). For each cluster, aspect ( $0-360^\circ$ ) was recorded and the terrain shape (no slope, convex or concave slope) was noted. Soil cores were not placed on slopes steeper than  $30^\circ$ . The middle cluster of soil cores in each experimental plot was instrumented with one Decagon 5-TM volumetric soil moisture and temperature sensor in a core of each soil type and one sensor placed nearby in the native soils (Fig. 2D). These sensors collected hourly data on soil surface temperature and volumetric soil moisture for the experiment duration (with some gaps due to damage by animals).

In each soil core, 20 lodgepole pine or 20 Douglas-fir seeds were planted  $\sim 0.25$  cm below the soil surface. Lodgepole pine seeds were collected from trees with serotinous cones at the lower edge of the lodgepole pine distribution in Yellowstone ( $\sim 2050$  m). Only cones that were  $> 3$  years old were harvested to ensure seeds were mature. Serotinous cones were dried at  $40^\circ\text{C}$  for 12 hours until they opened. Douglas-fir cones were collected in late August to late September from the upper edge of the species' distribution in Yellowstone (2,100 m - 2200 m). In 2014 Douglas-fir seeds were collected before cones were mature, leading to very low germination rates ( $< 1\%$  in the experiment). However, in 2015, Douglas-fir seed collection was successful. Once seeds were planted in experimental sites, hardware mesh (0.6 cm openings) was secured over the surface of the cores during the first season to deter granivory but still allow precipitation to fall unhindered. Once seedling establishment occurred, the mesh was removed so

seedling growth was not affected. During the experiment, all understory/herbaceous vegetation was regularly clipped around soil cores to minimize competition for light. At the end of each growing season during the experiment (2015-2017), we measured tree seedling establishment, mortality, seedling heights, and seedling basal diameters.

For both species, optimal germination was measured by germinating seeds in the lab at 21 °C in petri dishes with filter paper that was kept wet with deionized water. Overhead lights matched the daylength in Yellowstone during the growing season. The trials were run for one month. Optimal germination for lodgepole pine seeds in 2014 was 43 % and 62 % in 2015. Douglas-fir optimal germination in 2015 was 16 %. In 2014, Douglas-fir germination was not tested due to lack of seed (all was needed for experiment).

At the end of the experiment, we characterized weather conditions for growing seasons (May-August) between 2015 and 2017 (period during experiment where seedling establishment, mortality, and growth occurred) by analyzing records from weather stations near our low- and high-elevation experimental sites (Tower Junction, and Yellowstone Lake, respectively) (<https://www.ncdc.noaa.gov/>). We calculated daily growing season air temperature and cumulative precipitation during the growing season (amount of precipitation that accumulated since October 1<sup>st</sup> of the previous year) and we compared these values with 30-year normals (1981-2010) for each weather station.

#### *Controlled-environment experimental design*

In fall 2016, we conducted a split-block design experiment in a controlled-environment facility to better identify the specific combinations of growing season temperature and soil moisture that alter lodgepole pine and Douglas-fir regeneration. The experiment was conducted

in the Biotron, at the University of Wisconsin, Madison, which provides rooms where a range of environmental variables, including temperature, precipitation, and relative humidity, can be precisely controlled at a very fine temporal grain (e.g., minutes). We used these rooms to replicate historical and future growing seasons (June 15<sup>th</sup> to August 29<sup>th</sup>) in Yellowstone. The experiment included three temperature treatments: a historical (1955 to 2005), mid-21<sup>st</sup> century (2020 to 2050), and late-21<sup>st</sup> century (2050 to 2080) temperature period. Each temperature block was replicated three times (three separate controlled-environment rooms) for an  $n$  of 9. Within each temperature block, we applied five different precipitation treatments, representing wet to dry conditions. Eight 3.81-cm wide by 21-cm deep pots of rhyolite- and sedimentary-derived soils were assigned to each precipitation treatment. Pots received either 10 lodgepole pine or 10 Douglas-fir seeds. This yielded four replicate pots per temperature x precipitation x soil x tree species combination. The experiment ran for 75 days. For the first two weeks, soils were kept saturated to represent snow melt, and for the remainder of the experiment precipitation treatments were implemented. After one month, soil cores from the three replicate rooms of each temperature block were condensed into one room per temperature block, due to cost constraints.

*Temperature treatments:* Temperature treatments were developed based on gridded downscaled projections of current and future conditions from the IPCC 5<sup>th</sup> report (IPCC 2014). We selected the same GCMs used in the field experiment (albeit, the next generation). GCMs were forced with the representative concentration pathway 8.5 scenario, which assumes continued emissions increases through 2100 (Smith et al. 2016). GCMs were downscaled to 6-km resolution using the Multivariate Adaptive Constructed Analogs approach (Abatzoglou and Brown 2012) (<http://climate.nkn.uidaho.edu/MACA/index.php>). We selected historical and

future climate data for grid cells that corresponded to our three high-elevation field experiment sites (See field experiment section). Preliminary analysis suggested variance in the temperature data was orders of magnitude greater over time (e.g., year-to-year) than across space (between the three grid cells), so we pooled data from the three grid cells together.

To ensure historical and future temperature treatments tested effects of warming trends on seedling establishment, we translated gridded temperature projections into daily minimum and maximum growing season temperatures that could be replicated in a controlled-environment room. For the pooled grid cells, we calculated the median daily minimum and maximum temperature between June 15<sup>th</sup> and August 29<sup>th</sup> for each period (Fig. 3). We then fit linear trends to median minimum and maximum daily temperatures, which were then used as the minimum and maximum daily temperatures for each temperature treatment. Hourly relative humidity was calculated as the ratio of specific humidity to specific humidity at saturation, which varies with temperature.

Timing of daily minimum and maximum temperatures during the growing season was calculated using hourly temperature data recorded at a SNOTEL weather station (Thumb Divide-816) located near our high-elevation field experiment sites in Yellowstone between 1996 and 2015, the period for which data were available (<https://www.wcc.nrcs.usda.gov/snow/>). During the growing season, minimum and maximum daily temperatures most frequently occurred at 4:00 am and 1:00 pm, respectively. We set our minimum and maximum daily temperatures to happen at these times each day and linearly interpolated hourly temperature between the minimum and maximum. Length of day light was set using data from the Astronomical Applications Dept. of the U.S. Naval Observatory for the town of West Yellowstone.

*Precipitation treatments:* The sum of growing season precipitation varied little between historical and future growing seasons, consistent with other climate analyses of Greater Yellowstone (Westerling et al. 2011). To evaluate interactions between temperature and low precipitation conditions, we set experimental precipitation treatments by calculating the median (95.7 mm), 40<sup>th</sup> (81.1 mm), 30<sup>th</sup> (76.9 mm), 20<sup>th</sup> (72.2 mm) and 10<sup>th</sup> (53.7 mm) percentile growing season precipitation totals during the historical climate period (1955-2005).

The number of precipitation events per growing season was determined using the instrumental record of the same SNOTEL station that we used to determine timing of daily minimum and maximum temperature because precipitation was linearly apportioned among days in the gridded climate data (Livneh et al. 2013). We first calculated the median number of rain events ( $n = 14$ ) during growing seasons between 1988 and 2015. We then divided the sum of growing season precipitation in each treatment by 14 and scheduled watering events to occur evenly spaced through the growing season (every 4-5 days). We multiplied the per event precipitation amount in cm by the area of our pots (11.4 cm<sup>2</sup>) to calculate how much water each pot should receive in ml. Each pot received 4.3 ml, 5.8 ml, 6.2 ml, 6.6 ml, or 7.8 ml of water with a pipette every four to five days.

*Soils and seeds:* Soils derived from rhyolite or sedimentary parent materials were collected from the same recent fires where soil cores were taken for the field experiment. We harvested the top 20 cm of soil, passed it through a 2-mm sieve to ensure a consistent medium, and transported it to Madison, WI in sealed 5-gallon buckets. Soils were kept cool until used in the experiment by surrounding buckets with ice bags during transport and by storing them in walk-in refrigerators at the Biotron. The seeds used in this experiment were purchased from the

US Forest Service and collected in Greater Yellowstone. We selected seed stocks that were harvested at the same elevation as our low-elevation field experiment sites.

*Experimental measurements:* During the experiment, soil temperature and soil water potential were measured in one pot per temperature x soil type combination for three of the five precipitation treatment levels (driest, middle, wettest) every hour using Campbell Scientific 229 heat dissipation units. We measured soil water potential rather than volumetric soil moisture (as in the field experiment) to better characterize water balance that was physiologically meaningful to the tree seedlings. We were only able to measure soil water potential down to  $-2$  Mpa, due to equipment limitations, which is lower than the threshold for lodgepole pine seedling emergence (Petrie et al. 2016). Thus, some observations late in the experiment were not used to characterize moisture conditions, particularly on the sedimentary-derived soils. Every two to three weeks, we also tallied seedling emergence and mortality and measured seedling heights. We measured emergence instead of establishment (as we did in the field experiment), because we could visit the controlled-environment facility frequently. At the end of the experiment, all seedlings were collected, needles were counted, and root and shoot lengths were measured. Seedlings were then dried at  $60^{\circ}\text{C}$  for 24 hours, and root and shoot biomass were measured.

#### *Statistical analyses*

*Field experiment:* We used ANOVAs to explain factors influencing seedling establishment (% of planted seeds that established as seedlings) ( $n=263$ ), mortality (% of established seedlings that died) ( $n=111$ ), and size (height and basal diameter) (mm) ( $n=61$ ) at the end of the experiment. Soil cores from 2014 with Douglas-fir seeds were excluded from analysis because of the unsuccessful seed collection (see field experiment design). Analyses of seedling



mortality and size were only conducted using high-elevation cores because all seedlings died at low elevations. The unit of analysis was the individual soil core. We felt confident that this was appropriate because cores with the same soil and tree species were always separated by at least 50 m. Establishment and mortality were logit transformed prior to analysis and the other response variables were log transformed as needed to meet analysis assumptions. For all response variables, we evaluated the need to use linear mixed effects models (LMMs) to control for experimental site and year planted (seedling cohort) as a random effect with a likelihood ratio test. If necessary, LMMs were conducted using the lme4 package in R (Bates et al. 2015). Exhaustive model selection (Burnham and Anderson 2002) was conducted in all analyses to determine the most important variables using the R package MuMIn (Barton, 2015). All top models are presented ( $AIC_c < 2$ ). Analyses were conducted in R statistical software (R Development Core Team 2016). Means  $\pm$  SE are presented in results.

*Controlled-environment experiment:* ANOVAs were also used to determine what best explained seedling emergence (% of planted seeds that emerged as seedlings) ( $n=180$ ), mortality ( $n=146$ ), height (mm) ( $n=119$ ), needle number ( $n=119$ ), total biomass (mg) ( $n=120$ ), root-to-shoot length ratios ( $n=120$ ), and root-to-shoot biomass ratios ( $n=120$ ). Here, the unit of analysis was the average response variable value across the four temperature x precipitation x soil type x tree species replicate pots. For all response variables we evaluated the need to use linear mixed effects models (LMMs) to control for experimental room as a random effect with a likelihood ratio test. If necessary, LMMs were conducted using the lme4 package in R (Bates et al. 2015). Emergence and mortality were also logit transformed prior to analysis and the other response variables were log transformed as needed to meet analysis assumptions. We followed the same

analysis approach as in the field experiment (exhaustive model selection and reporting top models). Means  $\pm$  SE are presented in results.

## RESULTS

### *Field experiment*

*Climate:* During the portion of the experiment where seedling establishment, mortality, and growth occurred (2015 to 2017), daily growing season (May 1<sup>st</sup> to September 1<sup>st</sup>) air temperatures at the high-elevation experimental sites ranged from -2.5 °C to 19 °C with a median of 10.6 °C (Fig. 4A). Daily growing season soil surface temperatures were generally warmer than air temperature (median = 15.1 °C) and had a wider range (0.5 °C to 30 °C) (Fig. 4B). At the low-elevation experimental sites, daily air and soil temperatures were 2 °C to 3 °C warmer than at high elevations. Median air temperature was 13.1 °C and temperatures ranged from -0.5 °C to 22 °C (Fig. 4A). Soil surface temperatures were substantially warmer than air temperature (median = 17.1 °C), and ranged from 3.9 °C to 24.5 °C (Fig. 4B). At both elevations, growing season air temperatures between 2015 and 2017 were consistent with 30-year normals (1981-2010) (Fig. 4A).

Cumulative water-year (October 1<sup>st</sup> to September 30<sup>th</sup>) precipitation (i.e., the sum of daily precipitation received since October 1<sup>st</sup> of the previous year) at the high-elevation experimental sites was 362 mm in 2015, 419 mm in 2016, and 724 mm in 2017 (Fig. 4C). Median daily growing season volumetric soil moisture at high-elevation experimental sites was 16.9 % and ranged from 7 % to 27 % (Fig. 4D). Low-elevation sites received substantially less precipitation than high-elevation sites during the water year (302 mm in 2015, 263 mm in 2016, and 319 mm in 2017) (Fig. 4C) and daily volumetric soil moisture was on average 5 percentage points drier

than at high-elevations (median = 11.8 %, range = 4 % to 22 %) (Fig. 4D). Precipitation in 2015 and 2016 was consistent with 30-year normals at both elevations. In 2017, precipitation was 85 % greater than the 30-year normal at high-elevation sites and 16 % greater at low-elevation sites (Fig. 4C). However, precipitation anomalies in 2017 did not translate into meaningful differences in soil moisture (Fig. 4D).

*Edaphic conditions:* Soil cores derived from rhyolite (texture = 38 % sand, 43 % silt, 19 % clay) were less sandy than cores of sedimentary-derived soil (texture = 70 % sand, 19 % silt, 11 % clay). Rhyolite-derived soils were also more acidic than the sedimentary-derived soils (soil pH = 4.8 vs. 6.4), had more total N (0.11 % vs. 0.08 %), and had less available phosphorous (46 mg kg<sup>-1</sup> vs. 144 mg/kg<sup>-1</sup>), potassium (210 mg kg<sup>-1</sup> vs. 306 mg kg<sup>-1</sup>), and calcium (772 mg kg<sup>-1</sup> vs. 1,542 mg kg<sup>-1</sup>). Rhyolite and sedimentary soils were similar in organic matter (3.0 % vs. 2.5 %), and magnesium (170 mg kg<sup>-1</sup> vs. 180 mg kg<sup>-1</sup>).

*Topographic conditions:* At high-elevation experimental sites, approximately half of the soil cores were planted on slopes with xeric aspects ( $n = 80$ ), and a quarter were planted on mesic or flat aspects ( $n = 43$  and  $45$ , respectively). Of the soil cores planted on slopes, most were placed in convex positions ( $n = 60$ ) and fewer were in concave positions ( $n = 24$ ). At low elevations, 44 % of cores were planted on flat aspects ( $n = 74$ ), 29 % were planted on mesic aspects ( $n = 48$ ) and the rest were located on xeric aspects ( $n = 44$ ). Of the cores planted on slopes at low elevations, roughly half were located in convex positions and the other half in concave positions ( $n = 32$  and  $28$ , respectively).

*Seedling establishment:* During the field experiment, 378 lodgepole pine seedlings and 65 Douglas-fir seedlings established. All seedling establishment occurred by the end of the first

growing season following planting (2015 or 2016). Percent establishment in cores ranged from 0 % to 55 % of planted seeds. Variation in establishment was primarily explained by elevation (Table 1). On average, 12 times more lodgepole pine seedlings established in cores at high elevations (mean establishment =  $19 \% \pm 1.5 \%$ ) compared to cores at low elevations (mean establishment =  $1.6 \% \pm 0.4 \%$ ) (Fig. 5A) and four times more Douglas-fir established in high-elevation cores (mean establishment =  $5.4 \% \pm 0.9 \%$ ) versus low-elevation cores (mean establishment =  $1.3 \% \pm 0.5 \%$ ) (Fig. 5B). Lodgepole pine seedling establishment declined non-linearly with warming temperature and reduced soil moisture across elevation treatments; very little establishment occurred if average daily soil temperature was above  $16^{\circ}\text{C}$  (Fig. 5B) or soil moisture was below  $\sim 15\%$ . Establishment also varied by aspect (Table 1). Fewer seedlings of both species established in cores located on flat or xeric aspects (mean establishment =  $7.4 \% \pm 1.1 \%$ ) versus mesic aspects (mean establishment =  $12.4 \% \pm 1.9 \%$ ) (Fig. 6A). At low elevations, 92 % of the seedlings that established were in cores located on mesic or flat aspects.

*Seedling mortality:* By the end of the experiment, 201 (53 %) of the lodgepole pine seedlings and 48 (73 %) of the Douglas-fir seedlings had died. No seedlings that established at low elevations survived to the end of the experiment. However, some lodgepole pine seedlings planted on a north-facing aspect lived for three years (Fig. 7A). By the end of the experiment at high elevations, percent mortality in cores ranged from 0 % to 100 %. Mortality at high elevations varied primarily by species (Table 1). On average, 50 % lodgepole pine and 72 % of Douglas-fir died (Fig. 7). Aspect was also influential (Table 1). High-elevation seedlings of both species were 1.75 times more likely to die in cores located on xeric or flat aspects (mean mortality =  $65 \% \pm 6 \%$ ) relative to mesic aspects (mean mortality =  $37 \% \pm 7 \%$ ) (Fig. 6B).

*Seedling size:* At high-elevation sites where seedlings survived to the end of the experiment, variation in height was explained only by species (Table 1). Lodgepole pine seedlings were taller than Douglas-fir seedlings (lodgepole pine mean height =  $49 \pm 1.3$  mm, range = 19 mm to 112 mm; Douglas-fir mean height =  $35.4 \pm 2.9$  mm, range 20 mm to 50 mm). Basal diameters did not differ by species and averaged  $0.6 \pm 0.4$  mm (range 0.2 mm to 1.8 mm). No other variables explained variation in basal diameter (Table 1).

#### *Controlled-environment experiment*

*Temperature and soil moisture:* During the experiment, daily air temperature was coolest in the historical treatment, ranging from 10 °C to 18 °C (median = 11.5 °C) and relative humidity varied between 59 % and 81 % (median = 74 %). Temperatures in the early-21<sup>st</sup> century treatment were approximately 2 °C warmer than the historical treatment, with a median of 13.5 °C and ranging from 9 °C to 20 °C. Daily relative humidity varied from 42 % to 77 % (median = 69 %). In the mid-21<sup>st</sup> century treatment, temperatures were 4 °C warmer than the historical treatment (median air temperature = 15.8 °C) and ranged from 13 °C to 23 °C. Relative humidity varied between 36 % and 77 % (median = 66 %).

Growing season soil surface temperatures nearly matched air temperature in the controlled-environment experiment, likely because pots were narrow and not insulated from surrounding air. In the historical treatment, median soil surface temperature was 12.6 °C and ranged from 10.6 °C to 19.3 °C. Median daily soil water potential was -0.37 Mpa and varied between -1.8 Mpa and -0.03 Mpa. In the early-21<sup>st</sup> century treatment, growing season soil surface temperatures were more than 2.5 °C warmer than the historical treatment, with a median value of 15.3 °C and ranging between 13.5 °C and 19.3 °C. However, daily soil water potential

was similar to the historical treatment, with a median of -0.37 Mpa (range = -1.5 Mpa to -0.04 Mpa). In the mid-21<sup>st</sup> century treatment, growing season soil surface temperatures were substantially warmer (median = 16.3 °C, range from 14.3 °C to 24.8 °C). Daily soil water potential varied between -1.95 Mpa and -0.03 Mpa (median = -0.32 Mpa). Regardless of temperature treatment, soil type was a critical determinant of soil water potential. Pots of rhyolite-derived soil were generally wetter (median = -0.31 Mpa) than pots with sedimentary-derived soil (median = -0.49 Mpa).

*Seedling emergence:* During the experiment, 541 lodgepole pine and 366 Douglas-fir emerged. Average percent emergence ranged from 0 % to 40 % among experimental replicates. Variation in emergence was primarily explained by soil type, with approximately three-times more seedlings emerging in pots of rhyolite-derived soil than sedimentary-derived soil (Table 2, Fig. 8A). Emergence also varied by species (Table 2) and was greater for lodgepole pine (mean = 12.8 %  $\pm$  1.2 %) than for Douglas-fir (mean = 8.7 %  $\pm$  0.9 %). Emergence of both lodgepole pine and Douglas-fir seedlings was also modestly enhanced under mid-21<sup>st</sup> century temperature conditions (Table 2, Fig. 8B), which were 2 °C to 4 °C warmer than historical and early-21<sup>st</sup> century treatments and comparable to soil surface temperatures in the high-elevation treatment of the field experiment (Fig. 4B). Watering treatment did not influence seedling emergence (Table 2).

*Seedling mortality:* By the end of the experiment, 182 (34 %) of the lodgepole pine seedlings and 155 (42 %) of the Douglas-fir seedlings had died. Most variation in seedling mortality was explained by temperature period (Table 2). Few seedlings of both species died under historical temperature conditions (mean mortality = 14.5 %  $\pm$  2.5 %), but percent mortality

increased substantially as temperatures warmed in the early-21<sup>st</sup> century (mean mortality = 27.4 %  $\pm$  2.6 %) and mid-21<sup>st</sup> century (mean mortality = 29.7 %  $\pm$  2.7 %) treatments (Table 2, Fig. 8D). Mortality also varied with the density of seedlings in a core (Table 2); greater mortality was observed in dense pots (Fig. 9). Percent mortality within experimental replicates ranged from 0 % to 100 % and was similar between species (Douglas-fir mean = 26.7 %  $\pm$  2.3 %; lodgepole pine mean = 22.8 %  $\pm$  2.2 %). Percent mortality did not differ with watering treatment or soil types (Table 2, Fig. 8C).

*Seedling height and needle number:* By the end of the experiment, lodgepole pine seedling heights averaged 24.9 mm  $\pm$  0.7 mm (range = 12 mm to 45 mm) and Douglas-fir seedling heights averaged 19.8 mm  $\pm$  0.5 mm (range = 11 mm to 28 mm). Variation in seedling height was largely due to species differences and the interaction of species with temperature (Table 2). Lodgepole pine seedlings grew taller under mid-21<sup>st</sup> century conditions compared to historical climate, whereas Douglas-fir height did not vary with temperature period (Table 2, Fig. 10A-B).

Variation in needle number was largely explained by differences in temperature (Table 2), with more needles produced by both species under warmer temperature conditions (Fig. 10A-B). Under historical conditions, lodgepole pine and Douglas-fir produced similar numbers of needles (6.0  $\pm$  0.4). Under mid-21<sup>st</sup> century conditions, lodgepole pine produced more needles than Douglas-fir seedlings (16.2  $\pm$  0.9 vs. 10.9  $\pm$  0.6) (Table 2, Fig. 10B).

*Seedling total biomass:* Total biomass ranged from 2.6 mg to 40.6 mg and did not differ by species (mean = 13.8 mg  $\pm$  1.1 mg) (Table 2). Total biomass increased substantially with warming, from 7.8 mg  $\pm$  0.8 mg in the historical temperature treatment, to 10.6 mg  $\pm$  0.9 mg in

the early-21<sup>st</sup> century period and  $20.0 \text{ mg} \pm 1.1 \text{ mg}$  in the mid-21<sup>st</sup> century treatment (Table 2, Fig. 10C). There was a slight effect of watering treatment on Douglas-fir seedling biomass but not for lodgepole pine (Table 2). Total biomass also did not differ with soils (Table 2, Fig. 10C).

*Seedling root-to-shoot ratios:* Root-to-shoot biomass ratios did not differ between species (Table 2) but increased with warming, averaging  $0.4 \pm 0.02$  under historical temperature treatments and  $0.7 \pm 0.06$  in early-21<sup>st</sup> century and mid-21<sup>st</sup> century temperature treatments (Table 2, Fig. 10D). Root-to-shoot biomass ratios did not differ between soil types (Table 2, Fig. 10D).

Root-to-shoot length ratios differed between species, with smaller ratios for lodgepole pine (mean =  $1.6 \pm 0.1$ ) than Douglas-fir ( $2.1 \pm 0.2$ ) (Table 2). However, most variation in root-to-shoot length ratios was explained by temperature. Root-to-shoot length ratios were close to one under historical conditions (Douglas-fir mean =  $1.3 \pm 0.3$ , lodgepole pine mean =  $0.9 \pm 0.2$ ), increased modestly under early-21<sup>st</sup> century conditions (Douglas-fir mean =  $1.8 \pm 0.3$ , lodgepole pine mean =  $1.3 \pm 0.2$ ), and more than doubled under mid-21<sup>st</sup> century conditions (Douglas fir mean =  $2.9 \pm 0.3$ , lodgepole pine mean =  $2.1 \pm 0.1$ ) (Table 2, Fig. 10E). In addition, root-to-shoot length ratios of both species were nearly twice as large on sedimentary- versus rhyolite-derived soils (Table 2 Fig. 10E). Watering treatment did not influence root-to-shoot length ratios.

## DISCUSSION

These experiments provide mechanistic insights into potential effects of climate change on postfire tree regeneration, a life history stage that is critical for resilience of subalpine forests



to high-severity fire. In particular, our results identified the range of temperature and soil-moisture conditions in which lodgepole pine and Douglas-fir seedlings can establish in postfire soils. In our field experiment, an increase of just 2 °C in median daily soil surface temperatures (from 15.1 °C to 17.1 °C) and a five-percentage point decrease (from 16.9% to 11.8%) in median daily soil moisture led to enormous declines in seedling establishment for both species. Further, no seedlings survived three growing seasons at low-elevation sites with warm-dry conditions comparable to those projected for mid-century in the current subalpine forest zone. In our controlled-environment experiment, where daily soil surface temperatures were cooler (11.5 to 15.7 °C), warming led to increased tree seedling establishment, as might be expected with projected warming at upper treeline or higher latitudes. Integrating results from both experiments, the range of median daily growing season temperatures in which seedling establishment occurred (approximately 5.5 °C) was surprisingly narrow. At the warm end, drying reduced seedling densities nonlinearly, whereas at the cool end of the range, warming led to increased seedling densities. (Fig. 11). In both experiments, seedling establishment was also influenced by topo-edaphic heterogeneity, especially soils and aspect. Collectively, this study demonstrates how high-severity fire and postfire climate can interact to exert strong control over a key origin mechanism associated with 21<sup>st</sup> century subalpine forest resilience.

#### *Climate thresholds of tree regeneration*

We identified thresholds of growing season temperature (~ 16 °C) and soil moisture (~15%) associated with nonlinear changes in postfire establishment of subalpine conifer seedlings. Tree seedling establishment and survival is co-limited by soil moisture and temperature, so effects of climate change on postfire tree regeneration will emerge from complex

tradeoffs between warming and drying at very fine spatial and temporal scales (Anderson-Teixeira et al. 2013, Kroiss and HilleRisLambers 2015, Kueppers et al. 2017, Lazarus et al. 2018). In the beginning of life, tree seedlings must establish and survive with little accumulated carbon – there is small margin for error (Johnson et al. 2011). Warming conditions enhance carbon gain by increasing rates of photosynthesis and reducing frost damage on leaf and root tissues (Inouye 2000, Walck et al. 2011). In contrast, drying soils can reduce carbon assimilation by causing stomatal closure and hydraulic failure (Moyes et al. 2013, Reinhardt et al. 2015). The relative importance of these factors can change over time, even during a growing season. For example, temperature and soil moisture both limited carbon assimilation in first year limber pine seedlings in the Colorado Rocky Mountains (Moyes et al. 2015). However, temperature was limiting early during the growing season, and soil moisture was most important in middle and late summer (Moyes et al. 2015). Effects of warming and drying on establishment of individuals can also alter broader scale patterns of forest structure and tree species composition. For example, warming conditions in Yellowstone since 1988 enhanced survival of aspen that had previously established from seed at elevations far above their prefire distribution (Turner et al. 2003, Hansen et al. 2016). Following the 1988 fires, postfire regeneration of lower montane Douglas-fir was also greatly reduced on south-facing slopes (Donato et al. 2016), perhaps because soil temperature and moisture thresholds were surpassed.

Threshold responses to environmental drivers have been observed at multiple scales in forest ecosystems (Lenton et al. 2008, Hirota et al. 2011, Staver et al. 2011, Scheffer et al. 2012, Savage et al. 2013, van Nes et al. 2018), suggesting there are origin mechanisms potentially capable of initiating abrupt ecological change (Enright et al. 2014, 2015). However, nonlinear

responses can be extremely difficult to anticipate before thresholds are crossed because trees are long lived, which can mask the signal of impending change (Lloret et al. 2012, Hughes et al. 2013, Connell and Ghedini 2015). Seedling establishment and survival are more responsive to changing environmental conditions, though, and early postfire forest ecosystems may rapidly transition to different states that better match current conditions (Martínez-Vilalta and Lloret 2016, Mitchell et al. 2016). Reduced tree regeneration could signal slowing recovery rates after disturbance, and serve as a promising indicator of declining resilience (Dakos and Bascompte 2014, Allen et al. 2016, van de Leemput et al. 2018). Such information is very useful to inform proactive management strategies that consider forest resilience before fundamental state changes occur (Messier et al. 2015, Walker et al. 2016, Seidl et al. 2016). However, recovery rates are system specific, and long term studies of early post disturbance succession under contemporary conditions are necessary to provide critical baselines for comparison with future recovery (Turner et al. 1997, 2004, 2016).

In addition to warming and drying, factors not considered in these experiments could also alter postfire subalpine forest regeneration during the 21<sup>st</sup> century (Serra-Diaz et al. 2016). In particular, we explored effects of climate on seedling establishment and growth given a consistent seed supply. However, tree regeneration could be increasingly constrained if seed supply and delivery are reduced by more frequent and larger fires (Kemp et al. 2015, Harvey et al. 2016, Stevens-Rumann et al. 2018, Hansen et al. 2018) or by pre- or post-dispersal seed predation (Zwolak et al. 2010). Therefore, direct effects of warming on seedling establishment and survival must be placed within this broader ecological context.

*Warming and drying effects on morphological traits*

When seedlings survived, lodgepole pine and Douglas-fir responded to warming and drying by differentially allocating resources to roots, shoots, or needles, following patterns consistent with broader life history strategies (Franks et al. 2014, Smith et al. 2017). Seedlings generally produced more biomass and needles with warming, and root-to-shoot length ratios increased, with Douglas-fir increasing more than lodgepole pine. However, only lodgepole pine seedlings grew taller. Understanding differences in plant traits between and within species in response to climate change is important because it provides useful insights regarding the sets of conditions in which species may flourish and where species may be at a disadvantage, helping to identify climate mismatches (Münzbergová et al. 2017). Further, trait differences at the seedling stage can shape subsequent growth and survival (Tobner et al. 2013), in turn, influencing population and community level processes (Felton and Smith 2017). For example, Douglas-fir seedlings produced longer roots than lodgepole pine in our experiments. This may allow Douglas-fir to better survive 21<sup>st</sup> century postfire droughts in Yellowstone than lodgepole pine and lead to transitions in tree-species composition. Trait based frameworks seem to be a promising approach for better understanding climate change effects on forests (O'Brien et al. 2017). However, the drivers of variation in traits and associated consequences, particularly between individuals of the same species, are just beginning to be explored (Kerr et al. 2015, Siefert et al. 2015, Funk et al. 2017).

Given sufficient water, lodgepole pine seedlings allocated resources to height growth and needle production with warming, helping maximize light exposure under optimal conditions. Following fire, lodgepole pine tend to establish and grow very quickly (Turner et al. 2004),

prioritizing height growth (Coates 2000). As fires become more frequent at higher elevations in Yellowstone, these traits may confer advantage to lodgepole pine over other high-elevation conifer species because lodgepole pine could rapidly colonize burns and dominate early succession (Loehle 1998, Ettinger and HilleRisLambers 2017). However, having more needles during the seedling stage also increases transpiration demands (Moran et al. 2017) and prioritizing height growth appears to come at the expense of root length, both of which may disadvantage lodgepole pine seedlings as drought increases within their current distribution.

In contrast, Douglas-fir seedlings allocated resources to root length at the expense of height growth. Douglas-fir had larger root-to-shoot length ratios than lodgepole pine and the differences between species increased with soil drying and on sedimentary-derived soil with poor water holding capacity. Increasing root lengths and reduced needle number could help Douglas-fir seedlings tolerate drying conditions (Olmo et al. 2014), if they can establish. Deeper soils often better retain water through the growing season in semi-arid ecosystems (Stuart et al. 1989, Yaseef et al. 2010), providing a more consistent water source for seedlings with longer root systems (Kolb and Robberecht 1996, Blankinship et al. 2014). Douglas-fir also produce relatively large seeds, compared to lodgepole pine. This provides establishing seedlings with more carbohydrate reserves while establishing in hostile environmental conditions (Moles and Westoby 2004, Lazarus et al. 2018), as long as granivory does not limit seed supply (Zwolak et al. 2010).

#### *Origin mechanisms and future forest resilience*

This study offers insights into how patterns of postfire tree regeneration may shift in subalpine forests of western North America. As climate changes in the short term, it seems likely

that the influence of spatial and temporal variability in climate on postfire seedling establishment will grow (Fig. 11). Tree regeneration may be increasingly limited to mesic aspects, underlain by soils with higher water-holding capacity. Establishment events might also become limited to unusually cool-wet years (e.g., Andrus et al. 2018). Both would result in patchy forest cover and a coarsening of forest heterogeneity, where more xeric sites decrease in stand density or transition to non-forest. Within our field experiment, aspect exerted a secondary but meaningful influence on tree regeneration, and soil type was the primary determinant of establishment and mortality in the controlled-environment experiment. How aspect will mediate effects of climate change and shorter-term consequences for postfire forest regeneration needs further investigation, and field-based experimentation could be a promising approach.

In the longer term, it appears plausible that climate mismatches will occur where conditions in mid-21<sup>st</sup> century subalpine forests become incompatible with continued postfire establishment of the current suite of conifer species (Fig. 11) (Kueppers et al. 2017, Stevens-Rumann et al. 2018). This is largely consistent with species distribution models in Yellowstone that project upslope migration of lodgepole pine and Douglas-fir and decreases in suitable habitat (Crookston et al. 2010, Coops and Waring 2011, Gray and Hamann 2013, Hansen and Phillips 2015, Piekielek et al. 2015). Our results further suggest that both species could be well suited to shift their ranges upslope, which is also supported by evidence from the fossil pollen record, particularly for Douglas-fir. During the early- to mid-Holocene, when conditions were warmer and drier than today, Douglas-fir occupied areas at higher elevations than their current distribution (Whitlock 1993). However, Douglas-fir pollen was not observed in sediment cores from lakes where surrounding soils were derived from rhyolite, suggesting that edaphic

conditions may have constrained the species' distribution. We found that Douglas-fir established better on rhyolite-derived soils than on sedimentary-derived soils. Perhaps negative effects of rhyolite derived soils on Douglas-fir manifest during later life history stages (e.g., reduced nitrogen availability). Other factors, such as competition with lodgepole pine, dispersal limitations, and seed predation, could also influence longer-term persistence of Douglas-fir on rhyolite-derived soils in Yellowstone. To understand how Douglas-fir distributions may shift with future climate change, it will be critical to determine what factors mediate longer term persistence and growth.

#### CONCLUSION

Warming and drying trends are projected to continue over coming decades and may initiate origin mechanisms of abrupt change in forests following disturbances (Williams et al. 2013, Clark et al. 2016). Projected climate seems likely to cause marked change in tree seedling establishment, growth, and survival following stand replacing fires in subalpine forests of western North America. If seedlings survive, morphological traits will likely vary among species, following patterns consistent with broader life history strategies. Our results provide insights into how 21<sup>st</sup> century forests may change and the mechanisms that could underpin those responses. As environmental change accelerates, new experimental approaches that can elucidate origin mechanisms of abrupt ecological change will be essential. This paper illustrates how experimental treatments can be designed that more realistically represent climate-change drivers and how multiple experiments can be integrated to provide a more holistic perspective.

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# TABLES

Table 1. ANOVA results for top models ( $AIC_c < 2$ ) predicting establishment (%), mortality (%), seedling heights (mm) and basal diameters (mm) in the field experiment. Establishment and mortality were logit transformed. F-values (sum of squares) and significance levels are presented.

	Elevation	Soil type	Aspect	Terrain shape	Species	Elevation X species	Aspect X species	Terrain shape X species	Obs
Establishment									263
Model 1	220.7*** (242.6)		6.3** (13.8)		27.8*** (30.6)	27.1*** (29.8)			
Mortality									111
Model 1			4.9** (99.7)	2.4 (49.2)	8.0** (81.6)		3.2* (64.8)		
Model 2			4.8* (99.7)	2.4 (49.2)	7.9** (81.6)			2.6 (52.9)	
Model 3				4.0* (85.1)	6.7* (71.7)			3.6* (77.3)	
Model 4			4.7* (99.7)		7.7** (81.6)		2.4 (51.7)		
Model 5			4.7* (99.7)	2.3 (49.2)	7.7** (81.6)				
Height									61
Model 1					7.3** (0.5)				

Model 2	1.2 (0.1)		7.8** (0.5)	
Basal diameter				61
Model 1		2.7 (0.4)		
Model 2	2.2 (0.4)			
Model 3		2.9 (0.5)	1.3 (0.1)	
Model 4	1.9 (0.3)	2.3 (0.4)		
Model 5			0.9 (0.08)	

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\* P < 0.05, \*\* P<0.01, \*\*\* P<0.001

Table 2. ANOVA results for top models (AICc < 2) predicting emergence (%), mortality (%), heights (mm), needle number, total biomass (mg), root-to-shoot biomass ratio, and root-to-shoot length ratio in the controlled-environment experiment. Establishment and mortality were logit transformed and root-to-shoot length ratio was log transformed. F-values (sum of squares) and significance levels are presented.

	Temp. period	Soil type	Emerg.	Watering	Species	Temp. species	Temp soil type	Temp Emerg.	Emerg. soil type	Emerg. species	Species watering	Species soil type	Obs
<b>Emergence</b>													180
Model 1	9.5** (9.8)	219.0*** (112.6)			20.2** (10.4)		6.1** (6.2)						
<b>Mortality</b>													146
Model 1	14.5*** (60.1)		7.5** (15.5)		1.2 (2.6)								
Model 2	15.0*** (60.1)		7.7** (15.5)	2.1 (17.1)	1.3 (2.6)								
Model 3	14.3*** (60.1)		6.2* (12.9)										

Model 4	14.6*** (60.1)	2.6 (5.3)	3.8 (7.8)			4.1* (8.4)	
Model 5	14.6*** (60.1)		7.5** (15.5)	1.2 (2.6)			1.7 (3.5)
Model 6	14.7*** (60.1)		7.6** (15.5)	1.2 (2.6)		1.9 (7.6)	
Model 7	14.8*** (60.1)		6.4* (12.9)	2.1 (17.1)			
Model 8	14.6*** (60.1)		7.5** (15.5)	1.2 (2.6)	1.6 (6.4)		
Model 9	14.4*** (60.1)		6.2* (12.9)			1.4 (6.0)	

#### Height

119

Model 1	5.2* (170.5)	4.7* (78.0)		43.8*** (721.7)	5.7** (188.2)		
Model 2	4.1 (139.5)		4.2* (71.3)	35.1*** (590.9)	4.4* (147.4)		

#### Needle #

119

Model 1	64.9***	5.2*		8.2**	12.4***
	(1425.3)	(57.1)		(89.9)	(271.5)
Model 2	64.6***	0.03		10.6**	13.4***
	1425.3	(0.3)		(116.5)	(295.6)
Model 3	63.6***			10.3**	11.9***
	1425.3			(115.0)	(266.5)

**Total biomass** 120

Model 1	18.4***	2.6*	0.3	4.2**
	(7.1)	(2.0)	(0.1)	(3.2)

**Root-to-shoot biomass** 120

Model 1	24.5***		
	(19.8)		
Model 2	25.8***	4.3*	
	(20.1)	(1.7)	
Model 3	19.9***	16.9***	8.2**
	(13.6)	(5.8)	(2.8)

**Root-to-shoot length** 119



Model 1	28.1*** (19.8)	13.2*** (4.6)	8.0** (2.8)	2.7 (0.9)
Model 2	27.8*** (19.8)	13.0*** (4.6)	7.9** (2.8)	

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\* P < 0.05, \*\* P<0.01, \*\*\* P<0.001

## FIGURE CAPTIONS

**Figure 1.** (A) Subalpine and boreal forests generally move through four phases of the adaptive cycle; release (occurrence of severe wildfire), reorganization (initiation of successional trajectory), exploitation (succession back to mature forest) and conservation (mature forest). (B) During the reorganization phase, forest ecosystems are vulnerable to hostile environmental conditions like drought that can initiate transitions to alternate states by causing tree regeneration failure. (Pictured; experimental pots of soil in which drought treatments have been implemented) (C) However, warming can also enhance tree establishment, particularly at the upper edge of tree species distributions (Pictured; Tree seedlings experiencing experimental warming) (D). If seedlings establish, intraspecific and intraspecific variation in seedling traits may determine which individuals survive and thrive under warming and drying conditions (Pictured; lodgepole pine seedling).

**Figure 2.** (A) Map of Yellowstone National Park (WY, USA) including the locations of field experiment sites. (B) Gridded climate showing the locations (green cells) in Yellowstone where recent moisture deficit (2002-2012) matches projected moisture deficit (2050-2060) in lodgepole pine forests. (C) Experimental plot layout. One plot was setup at each site in 2014 and another was setup at each site in 2015, separated from the first by > 100 m. (D) A cluster of instrumented soil cores at the center of an experimental plot.

**Figure 3.** Minimum and maximum daily temperatures between June 15<sup>th</sup> and August 29<sup>th</sup> used in the greenhouse experiment for the historical (1955-2005), early-21<sup>st</sup> century (2020-2050) and mid-21<sup>st</sup> century (2050-2080) temperature treatments. Minimum and maximum daily temperature values from each temperature period for three grid cells of three GCMs were pooled

(grey dots). The median values were quantified (squiggly lines) and a linear trend was fit to the median time series, which then served as minimum and maximum daily temperatures in the experiment.

**Figure 4.** (A) Median daily air temperature for the growing season from weather stations near high-elevation and low-elevation experimental sites. The horizontal lines show thirty-year normals (1981-2010) at the high- and low-elevation weather stations. (B) Median daily soil surface temperature for the growing season at high-elevation and low-elevation experimental sites. (C) Median cumulative annual precipitation during the growing season recorded at weather stations near the high-elevation and low-elevation experimental sites. The horizontal lines show thirty year normals (1981-2010) at the high- and low-elevation weather stations. (D) Median daily volumetric soil water content for the growing season at high-elevation and low-elevation experimental sites.

**Figure 5.** (A) Establishment (%) of lodgepole pine seedlings and Douglas-fir seedlings versus site level mean growing season soil surface temperature (°C) in the field experiment. Lines show a loess fit for lodgepole pine and a linear fit for Douglas-fir. (B) Establishment (%) of lodgepole pine seedlings and Douglas-fir seedlings in the field experiment as a function of elevation.

Values are means  $\pm$  2 standard errors.

**Figure 6.** (A) Establishment (%) and (B) mortality (%) of lodgepole pine and Douglas-fir seedlings in the field experiment as a function of aspect. Values are means  $\pm$  2 standard errors.

**Figure 7.** Cumulative mortality (%) of (A) lodgepole pine and (B) Douglas-fir during the field experiment broken out by elevation (low or high) and seedling cohort (2014 or 2015). Values are means  $\pm$  one standard error and the age of seedlings are provided for each data point.

**Figure 8.** Top panel: Seedling emergence (%) of Lodgepole pine and Douglas-fir in the controlled-environment experiment versus (A) soil type and (B) temperature period. Bottom panel: Seedling mortality (%) by the end of the experiment versus (C) soil type and (D) temperature period. Values are means  $\pm$  2 standard errors.

**Figure 9.** Mortality (%) of lodgepole pine and Douglas-fir seedlings in the controlled-environment experiment as a function of emergence (%) on sedimentary and rhyolite soil types. The distributions of seedling emergence on each soil type are also provided for comparison.

**Figure 10.** Lodgepole pine and Douglas-fir (A) seedling height, (B) needle number, (C) total biomass, (D) root to shoot biomass ratio, and (E) root to shoot length ratio as a function of temperature period and soil type. Values are means  $\pm$  2 standard errors.

**Figure 11.** The range of growing season temperatures in which lodgepole pine and Douglas-fir seedling establishment occurs in Yellowstone. In the green zone warming temperatures cause increased seedling density. In the beige zone warming and drying counter one another and secondary variables such as aspect are particularly important determinants of seedling density. In the brown zone, drying outweighs warming and seedling density declines quickly. Below the temperature distributions from the field and controlled-environment (CE) climate treatments are provided for context.

Figure 1.



Figure 2.

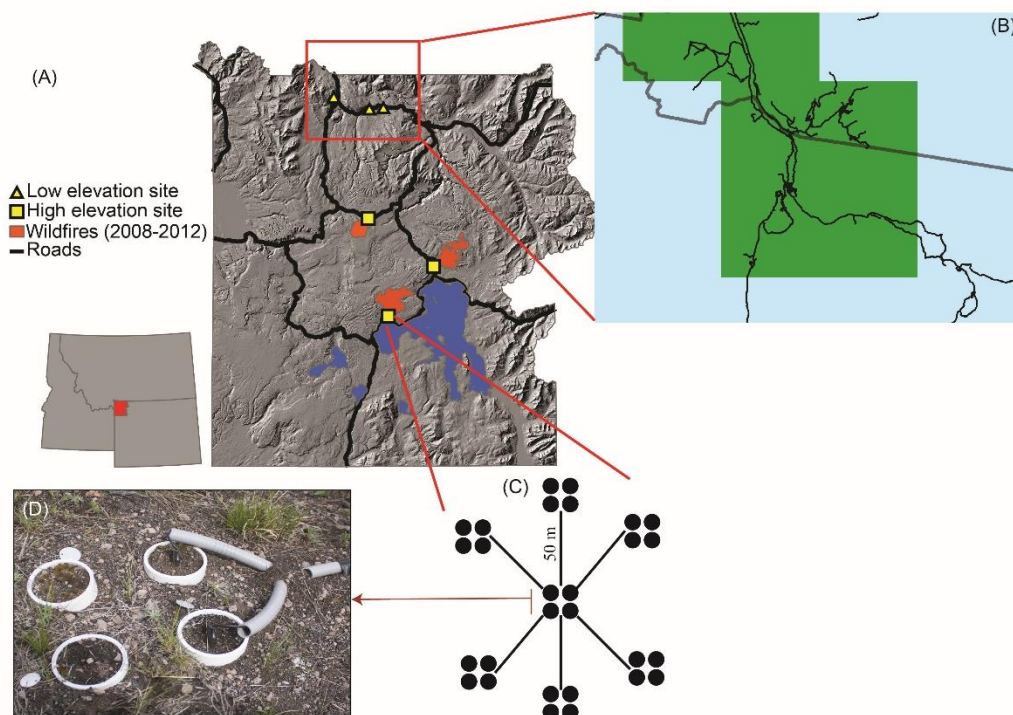


Figure 3.

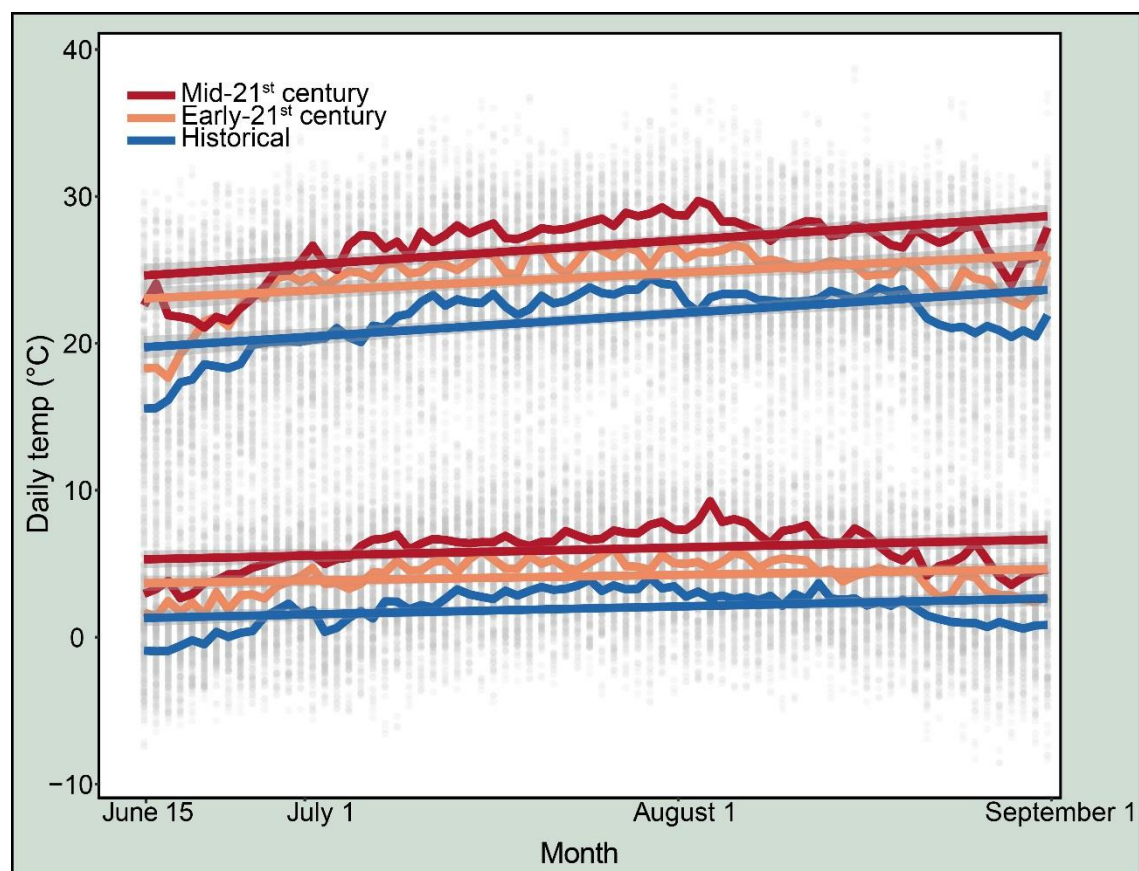


Figure 4.

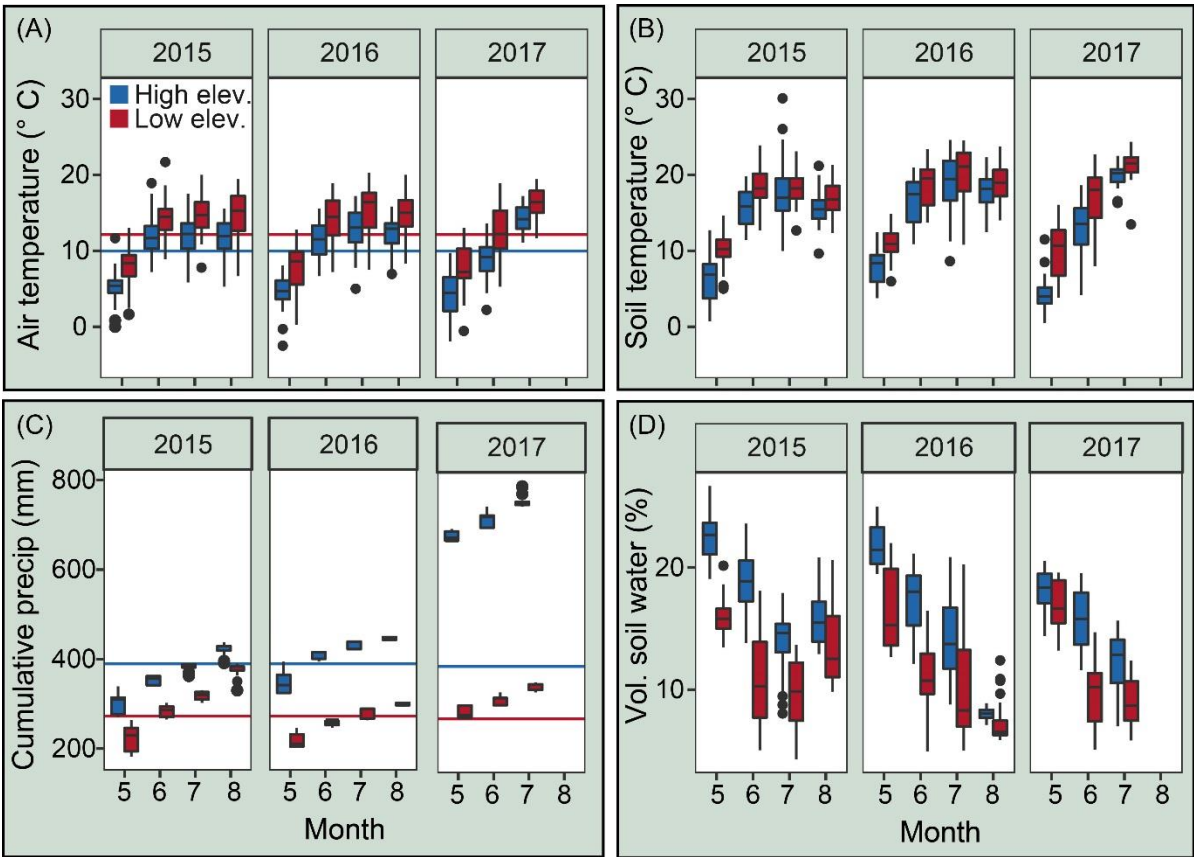




Figure 5.

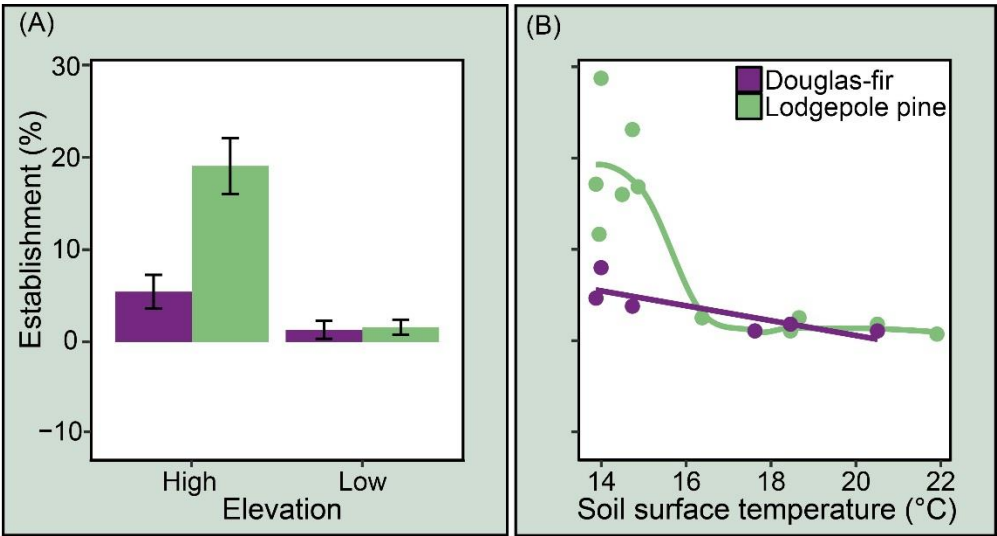


Figure 6.

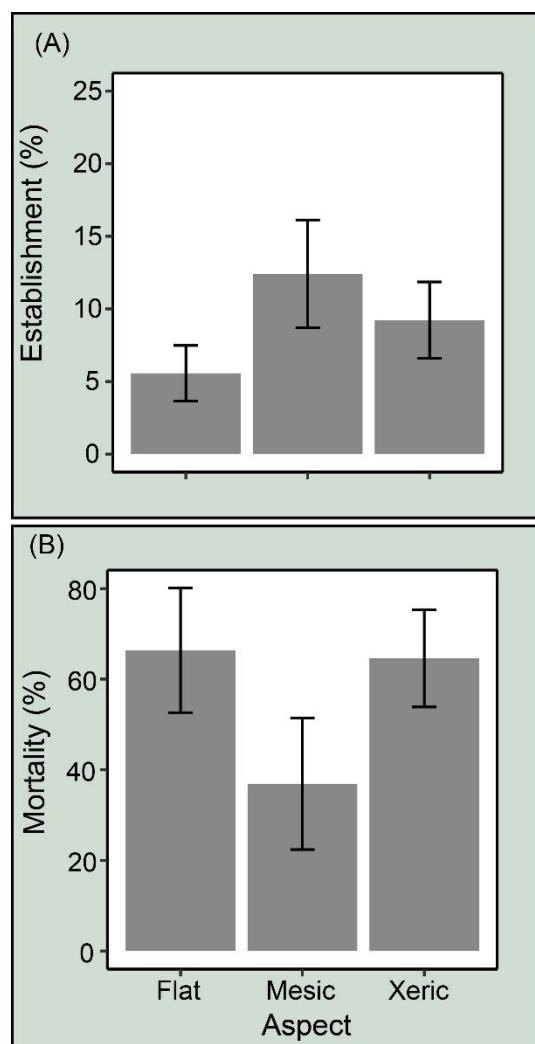


Figure 7.

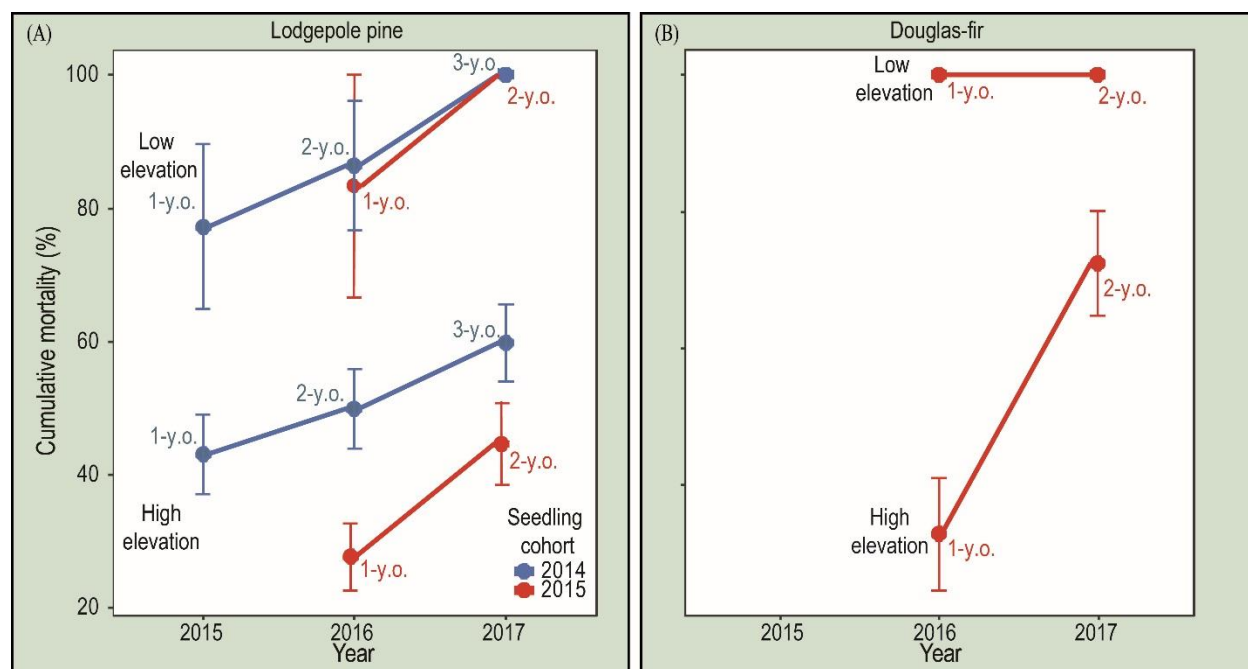


Figure 8.

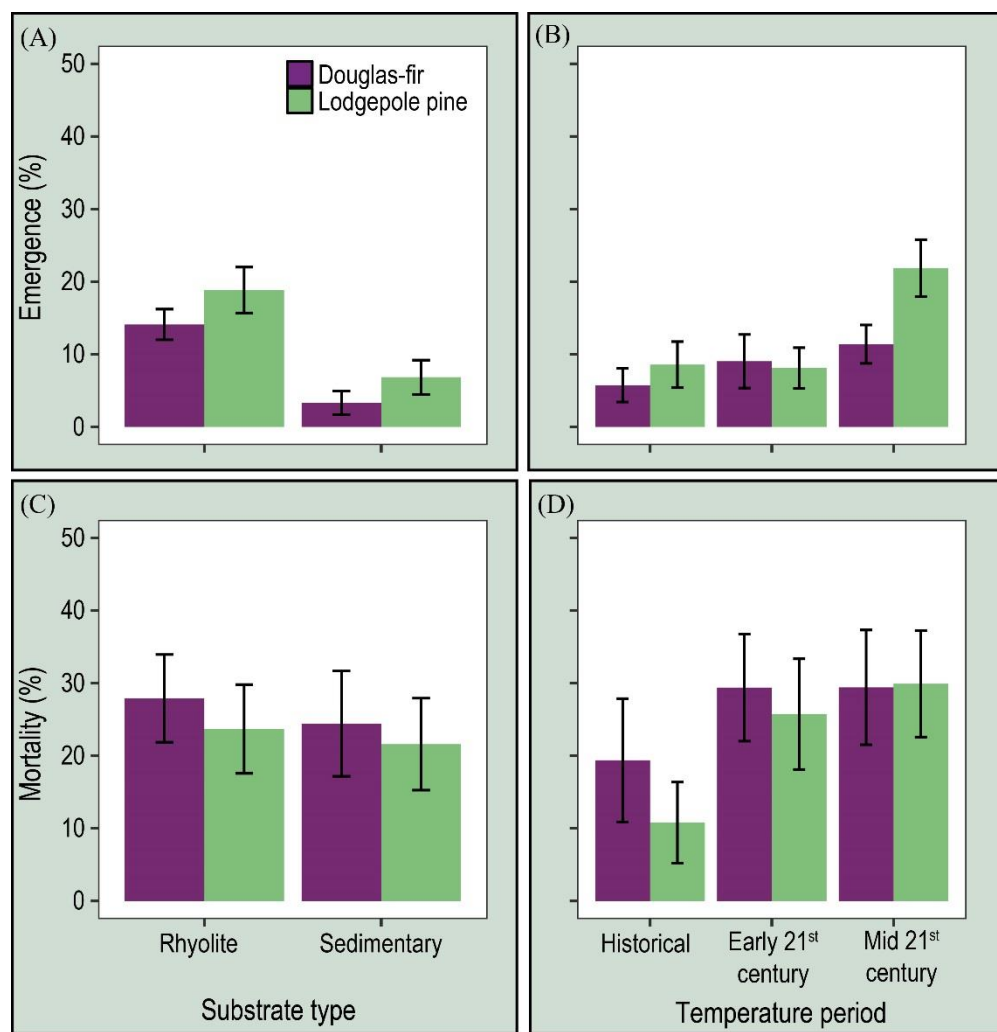


Figure 9.

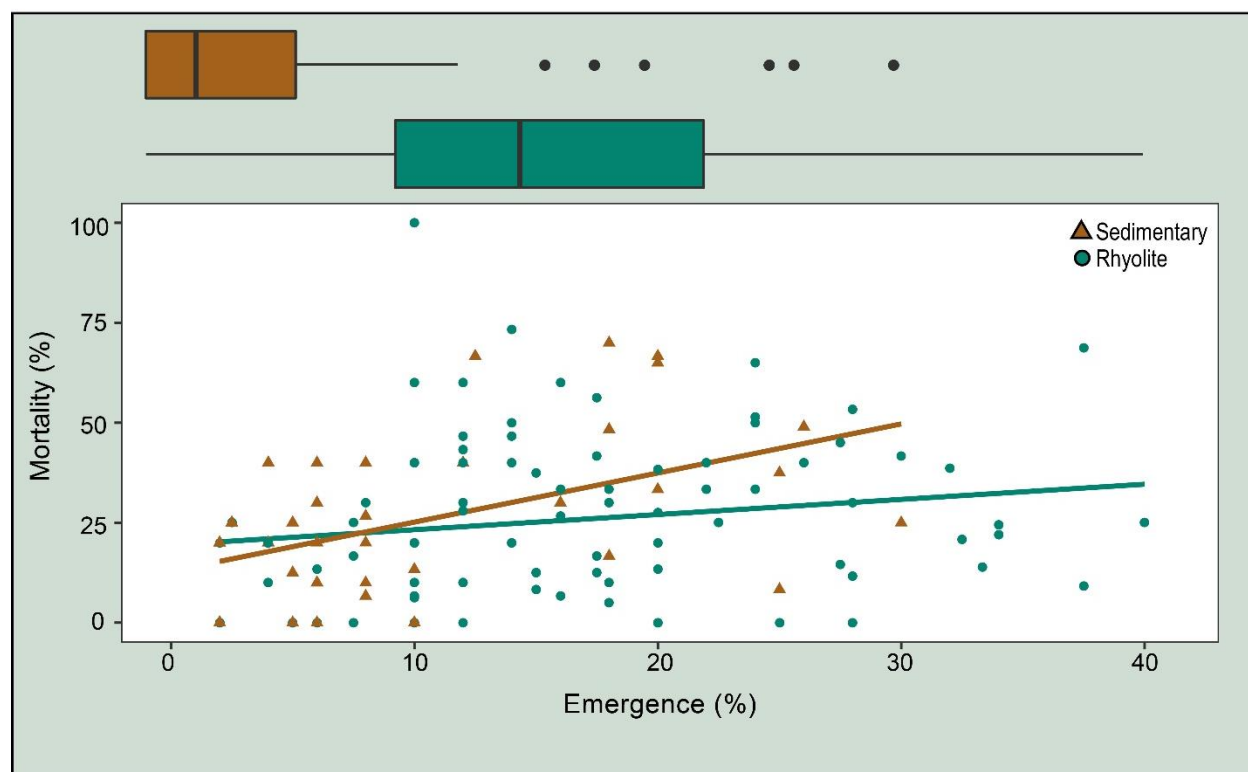


Figure 10.

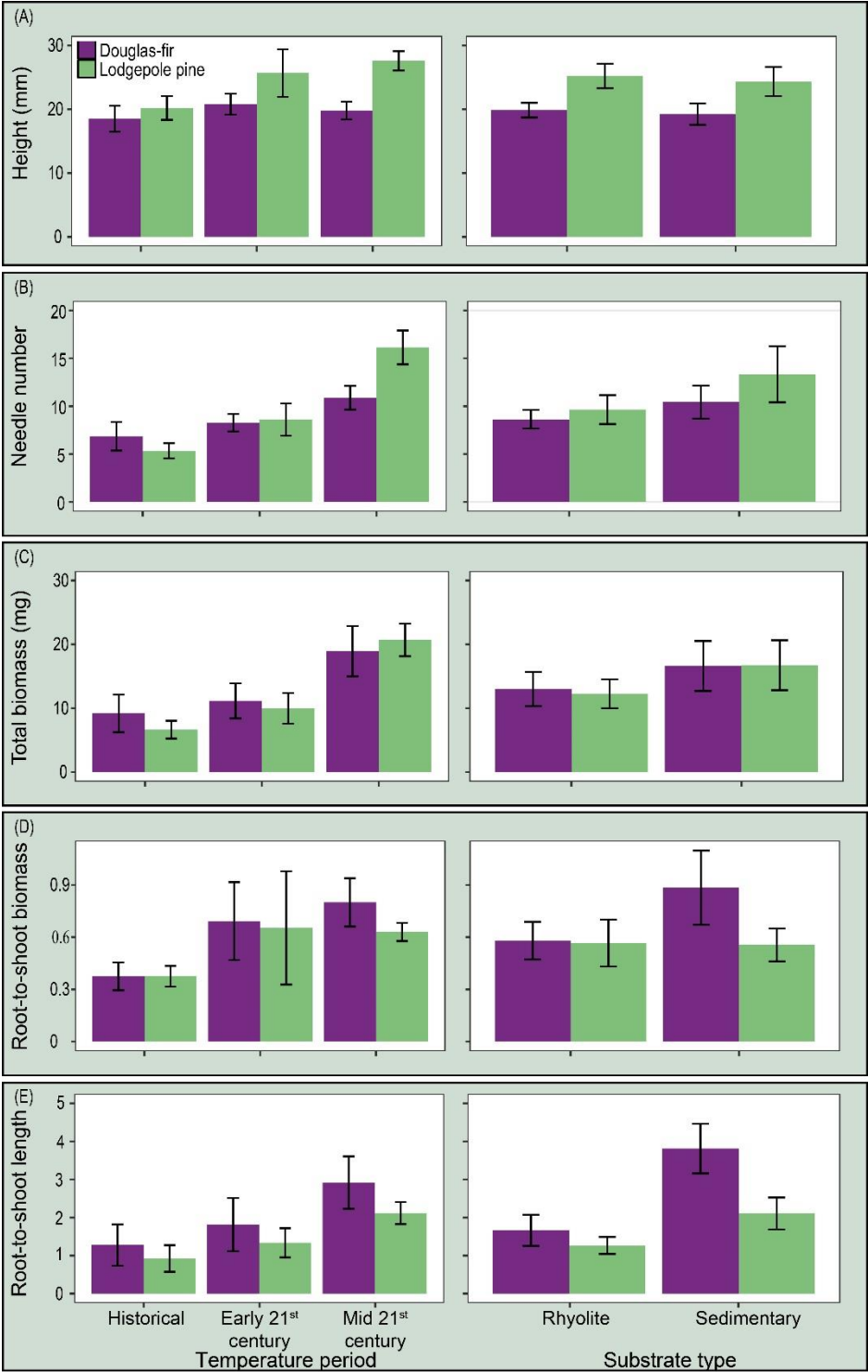
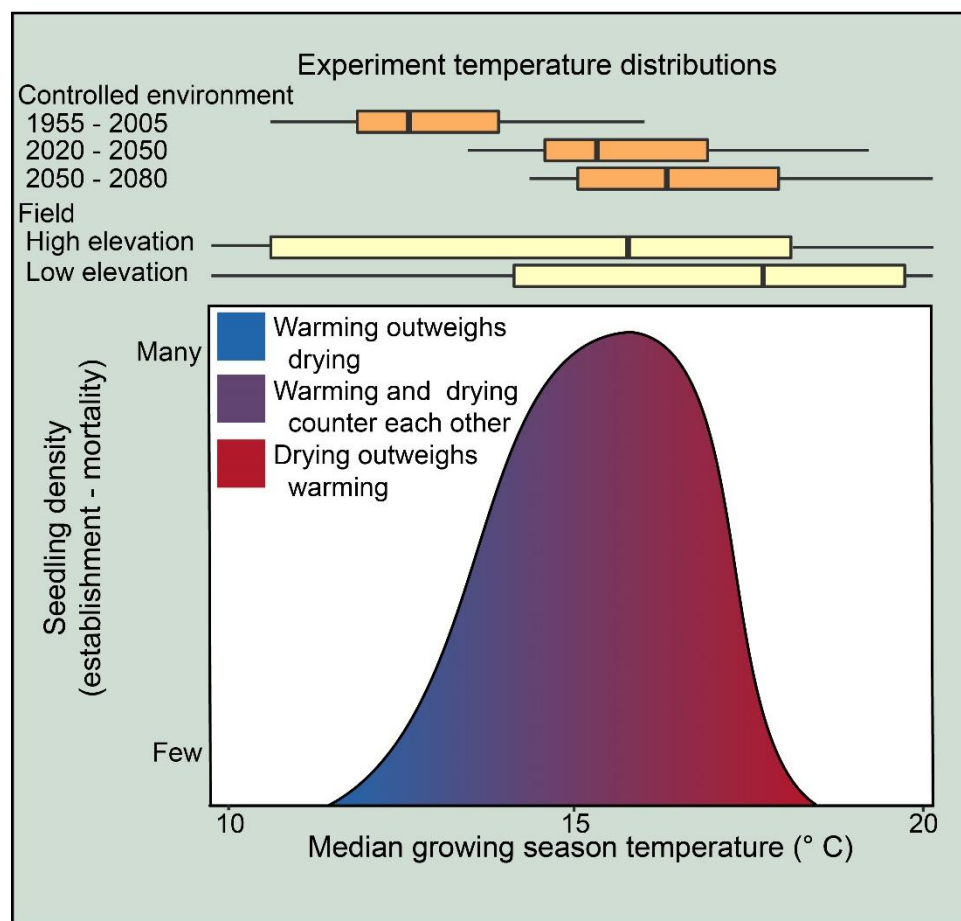


Figure 11.



**Chapter 3 – It takes a few to tango: Changing climate and fire regimes can cause  
regeneration failure of two subalpine conifers**

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## ABSTRACT

Environmental change is accelerating in the 21<sup>st</sup> century, but how multiple drivers may interact to alter forest resilience remains uncertain. In forests affected by large high-severity disturbances, tree regeneration is a resilience linchpin that shapes successional trajectories for decades. We modeled stands of two widespread western US conifers, Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and lodgepole pine (*Pinus contorta* var. *latifolia*), in Yellowstone National Park (Wyoming, USA) to ask: (1) What combinations of distance to seed source, fire return interval, and warming-drying conditions cause postfire tree-regeneration failure? (2) If postfire tree regeneration was successful, how does early tree density differ under future climate relative to historical climate? We conducted a stand-level (1 ha) factorial simulation experiment using the individual-based forest process model iLand to identify combinations of fire return interval (11 to 100 years), distance to seed source (50 to 1000 m), and climate (historical, mid-21<sup>st</sup> century, late-21<sup>st</sup> century) where trees failed to regenerate by 30-years postfire. If regeneration was successful, we compared stand densities between climate periods. Simulated postfire regeneration were surprisingly resilient to changing climate and fire drivers. Douglas-fir regeneration failed more frequently (55%) than lodgepole pine (28% and 16% for non-serotinous and serotinous stands, respectively). Distance to seed source was an important driver of regeneration failure for Douglas-fir and non-serotinous lodgepole pine; regeneration never failed when stands were 50 m from a seed source and nearly always failed when stands were 1 km away. Regeneration of serotinous lodgepole pine only failed when fire return intervals were  $\leq 20$  years and stands were far (1 km) from a seed

source. Warming climate increased regeneration success for Douglas-fir but did not affect lodgepole pine. If regeneration was successful, postfire density varied with climate.

Douglas-fir and serotinous lodgepole pine regeneration density both increased under 21<sup>st</sup>-century climate but in response to different climate variables (growing season length vs. cold limitation). Results suggest that given a warmer future with larger and more frequent fires, a greater number of stands that fail to regenerate after fires combined with increasing density in stands where regeneration is successful could produce a more coarse-grained forest landscape.

**Keywords:** *Climate change; Drought; Forest resilience; Process-based modeling; Seedling establishment; Wildfire; Succession; Yellowstone National Park*

## INTRODUCTION

Forests will experience increased stress as environmental change accelerates in the 21<sup>st</sup> century (Millar and Stephenson 2015, Trumbore et al. 2015). It remains poorly resolved whether forests will prove resilient and recover from these perturbations (Scheffer 2009) or instead transition to alternate states (Ghazoul et al. 2015, Reyer et al. 2015). Resilience is defined as the capacity of a system to absorb disturbances while retaining function, structure, feedbacks, and thus, identity (Walker et al. 2006). It is plausible that whole forested regions, such as the Amazon and boreal forest, may prove vulnerable to environmental change (Lenton et al. 2008, Hirota et al. 2011, Scheffer et al. 2012, Gauthier et al. 2015). Yet, quantifying forest resilience is challenging because multiple drivers, like natural disturbances, drought, land use, and nitrogen deposition will act on forests simultaneously, causing compound effects that are difficult to anticipate (Paine et al. 1998, Savage and Mast 2005, Staal et al. 2014, Buma 2015, Littell et al. 2016). Further, heterogeneity in abiotic conditions (e.g., substrate, elevation, aspect) and variation in tree functional traits (among and within species) can amplify or dampen driver effects (Lamont and Enright 2000, Chmura et al. 2011, Hoffmann et al. 2012, Johnstone et al. 2016). Thus, studies identifying interactions among multiple drivers that influence forest resilience could yield substantial insight into how and why 21<sup>st</sup>-century forests may change.

Regional forest change will likely emerge from the effects of environmental drivers on local- and landscape-scale processes (e.g., dispersal, seedling establishment, tree growth, competition, and mortality) (Peters et al. 2004, 2007, Turner 2010). In

forests where large wildfires kill most trees (i.e., stand-replacing fire), tree regeneration is a resilience linchpin (Turner et al. 1998, Johnstone and Chapin 2006, Johnstone et al. 2010, Savage et al. 2013) because seedling establishment in the first few years after disturbance dictates species composition and stand structure for decades to centuries (Kashian et al. 2005, Martínez-Vilalta and Lloret 2016). Robust postfire tree regeneration requires sufficient seed supply and delivery. Fire activity is projected to increase globally (Pechony and Shindell 2010, Seidl et al. 2014, 2017, Abatzoglou and Williams 2016) and postfire seedling densities may be reduced if burned patch sizes exceed effective dispersal distances or if multiple fires reoccur before trees reach reproductive maturity (Keeley et al. 1999, Enright et al. 2014, 2015, Kemp et al. 2016, Harvey et al. 2016a, Johnstone et al. 2016, Stevens-Rumann and Morgan 2016, Chambers et al. 2016). When seed is available, changing climate can also shape regeneration outcomes because tree seedlings are very sensitive to environmental conditions (Walck et al. 2011). Warming could reduce establishment if severe droughts follow fires (Clark et al. 2016, Harvey et al. 2016a) or warming could enhance establishment by reducing frost damage (Inouye 2000) and lengthening the growing season.

It is challenging to disentangle the effects of multiple drivers on postfire regeneration, but process-based models offer a promising approach when empirical studies cannot capture the full range of potential conditions. Large, short-interval fires and severe postfire droughts may become more prevalent in the western US (Westerling 2016) but still occur infrequently in subalpine forests. Thus, opportunities to observe in the field how combinations of changing fire and drought affect tree regeneration across

heterogeneous landscapes are scant. Further, the magnitude of projected 21<sup>st</sup>-century environmental changes, their complex interactions, and the potential for emergent feedbacks suggest that future ecosystem dynamics may be difficult to predict solely based on current observation (Gustafson 2013, Bowman et al. 2015). However, process-based models allow exploration of a more complete set of conditions than found in the field and should provide robust projections under novel conditions because they are based on ecological first principles rather than empirical relationships (Seidl et al. 2011, Keane et al. 2015, Gustafson 2013). Models also can help distill complex phenomena down to essential components and highlight gaps in ecological understanding (Grimm and Berger 2016, Dietze 2017, Seidl 2017).

Yellowstone National Park (Wyoming, USA) is an excellent place to study how changing climate and fire regimes may alter postfire tree regeneration. Subalpine forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*) experienced large stand-replacing fires at 100 to 300 year intervals during the Holocene (Millspaugh et al. 2000, Power et al. 2011). Postfire tree regeneration has generally been robust following fires (Turner et al. 1997, 2004, 2016). Some lodgepole pine trees in Yellowstone develop serotinous cones that remain closed and accumulate for many years; when heated by fire, they open and drop large quantities of seed. Other lodgepole pines produce only non-serotinous cones that open as they mature. (Tinker et al. 1994). Lower montane forests are dominated by more drought tolerant Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Warming and increased drought during the 21<sup>st</sup> century are projected to cause marked increases in the size, severity, and frequency of wildfires (Westerling et al. 2011)

and alter the environmental context in which trees reestablish. The magnitude of expected change may be inconsistent with current forest structure and tree-species composition, meaning that forests could change profoundly (Hansen and Phillips 2015, Clark et al. 2017).

We conducted a factorial simulation experiment to evaluate effects of changing fire regimes and postfire climate conditions in Yellowstone on regeneration of two widespread Rocky-mountain conifer tree species, lodgepole pine and Douglas-fir. We asked two questions. (1) What combinations of distance to seed source, fire return interval (FRI) and warming-drying conditions cause postfire tree-regeneration failure? We hypothesized that postfire regeneration failure would be more likely if seed delivery was reduced by increasing distance to seed source (i.e., a proxy of increasing fire size or changing perimeter shape), if seed supply decreased with shortened FRI because trees burned before reaching maturity, or if postfire drought reduced seedling establishment (Table 1). We also expected that lodgepole pine and Douglas-fir would differ in their responses. We hypothesized Douglas-fir regeneration would be most sensitive to distance to seed source because Douglas-fir produce fewer relatively heavy seeds and rely on adjacent unburned forests for seed delivery; non-serotinous lodgepole pine regeneration would show intermediate sensitivity because they produce a greater number of lighter seeds; and serotinous lodgepole pine regeneration would be least sensitive due to the canopy seedbank. However, we expected serotinous lodgepole pine to be very sensitive to shortened FRIs that burn stands before the canopy seedbank develops. (2) If postfire tree regeneration was successful, how does early postfire tree density differ under future

climate relative to historical climate? We hypothesized that, once trees established, their postfire densities would be sensitive to variation in climate such that increasing drought frequency and severity would be associated with reduced tree density. We also expected that early postfire Douglas-fir densities would be less affected by future drought than lodgepole pine because Douglas-fir are physiologically adapted to drier conditions.

## STUDY AREA AND METHODS

### *Study area*

Yellowstone National Park encompasses approximately 9,000 km<sup>2</sup> in northwestern Wyoming, USA. Elevation ranges from 1,600 m to 3,400 m, with lower tree line at 1,800 m and upper tree line at 3,050 m (Despain 1990). Climate is relatively warm and dry in the lower montane zone where Douglas-fir is common, with a mean July temperature of 17.5°C and 390 mm of annual precipitation (Western Regional Climate Center 2017). Climate is cooler and wetter in the higher-elevation subalpine zone, with a mean July temperature of 14°C and annual precipitation of 584 mm. Forest soils are generally derived from volcanic parent material, typically rhyolite or andesite. Rhyolite-derived soils have less mineral nitrogen (Whitlock 1993) and poor water holding capacity (Simard et al. 2012) compared to soils derived from andesite (Despain 1990), but both are considered infertile. Douglas-fir and lodgepole pine are obligate seeders, and in Yellowstone, both experience stand-replacing fire. Seeds are wind dispersed, and most seeds fall within 100 m of the source (Burns and Honkala 1990). Following the iconic 1988 Yellowstone fires, which burned two-thirds of the park, Douglas-fir and lodgepole pine both reestablished successfully, albeit with substantial variability across the

landscape. Early (24 year) post-1988 fire Douglas-fir stand densities ranged from 0 to 19,667 stems  $\text{ha}^{-1}$  with a median of 1,250 stems  $\text{ha}^{-1}$  (Donato et al. 2016); postfire (24 year) lodgepole pine densities ranged widely, from 0 to >340,000 stems  $\text{ha}^{-1}$  with a median density of 4,050 stems  $\text{ha}^{-1}$  (Turner et al. 2016). Stands where prefire serotiny was high account for the denser postfire regeneration. Stands where prefire serotiny was low had postfire densities ranging from 600 to 2,300 stems  $\text{ha}^{-1}$  (Turner et al. 1997, 2004).

### *Model overview and simulation experiment*

We simulated stand-level (1-ha) dynamics using an individual-based forest process model, iLand (Seidl et al. 2012, 2014). iLand simulates trees within a stand and uses a hierarchical framework wherein broader-scale processes emerge dynamically from interactions among individual trees (Seidl et al. 2012). iLand represents tree growth, mortality, and competition in response to canopy light interception, radiation, thermal conditions, soil water, and nutrient limitation. While climate and soil conditions are assumed to be spatially homogeneous within a stand (1 ha), variation in light is simulated at 2×2m horizontal resolution based on overstory structure and composition. Climate variability is considered at a daily temporal grain. iLand also simulates disturbances. Extensive model documentation is available online (<http://iland.boku.ac.at>). The model has been well tested and extensively used in the western United States (Seidl et al. 2012, 2014) and Europe (Pedro et al. 2015, Thom et al. 2017a, 2017b), and has recently been parameterized and evaluated for Yellowstone.



The model explicitly simulates tree regeneration based on seed production, seed dispersal, and effects of temperature, light, and soil-moisture conditions on seedling establishment and survival (Seidl et al. 2012) (Appendix S1). We extended the regeneration module of iLand in two ways. First, we added serotiny as a functional trait for lodgepole pine. Serotinous lodgepole pine only drop seeds in the year following a fire. When trees are serotinous, the amount of seed released is a multiple of the seeds produced by a non-serotinous tree, representing the accumulation of cones over multiple years. We further incorporated an effect of soil moisture on rates of seedling establishment in addition to the already existing temperature limitation. The probability of seedling establishment at a 2m cell is linearly scaled between a species-specific minimum soil water potential, where establishment does not occur, and field capacity, where establishment is not constrained by soil moisture. We evaluated the improved regeneration module of iLand and simulated tree establishment agreed well with independent field observations (Appendix S2).

*Initial stand structure.* Simulations were initialized with a representative monospecific stand for each forest type using median stem density and tree heights for each forest type as recorded 11 years after the 1988 Yellowstone fires (Turner et al. 1999, 2004, 2016, Donato et al. 2016). We chose not to vary initial stand structure within each forest type because we were interested in experimentally testing climate-fire interactions and therefore we minimized other sources of variation.

*Topoedaphic conditions.* Our simulations did include variation in substrate and elevation, because both influence tree establishment, and thus, are important for

addressing our questions. We simulated soils derived from two volcanic parent materials, rhyolite and andesite, which account for most of Yellowstone's subalpine landscape (Despain 1990). Relative fertility rating (calibrated within iLand to 45 and 55 for rhyolite and andesite, respectively, on a [0-100] scale) and soil texture (62% sand, 30% silt, 8% clay for rhyolite, 51% sand, 37% silt, 12% clay for andesite) were set according to representative soil surveys conducted throughout Yellowstone (Turner et al. 1999, Simard et al. 2012). For all soils, effective depth was set to 95 cm. Elevation was included by simulating stands at lower treeline (2,000 m), as well as the mid (2,300 m), and high elevation (2,600 m) of the subalpine zone. These span the elevational range in which Douglas-fir and lodgepole pine are found regionally.

*Factorial simulation experiment.* We conducted a factorial experiment using iLand to evaluate how combinations of climate and fire conditions affected early (30 year) postfire tree regeneration of Douglas-fir, non-serotinous lodgepole pine, and serotinous lodgepole pine. Thirty years was selected as a benchmark for assessing regeneration because it accommodates the more protracted establishment window of conifers that lack a canopy seedbank (Turner et al. 1999, Donato et al. 2016), captures longer-term effects of climate on young trees, and largely avoids the self-thinning that occurs in dense stands during later periods of stand development. The factors considered in the experiment for all forest types were FRI, distance to seed source, and variation in climate and they were applied to every combination of the two substrates and three elevations.

*Return interval for high-severity fire.* Effects of FRI were simulated by burning stands at age 11, 20, 50, or 100 yrs. Simulated FRI spanned the range from short-interval fires projected by the end of the 21<sup>st</sup> century (Westerling et al. 2011) and observed in Yellowstone (e.g., the 2000 Boundary Fire burned 12-yr old lodgepole pine that regenerated from the 1988 fires) to the lower end of FRIs observed during the Holocene (Millspaugh et al. 2000). Stand development was simulated until the specified FRI was reached, at which time stand-replacing fire killed all prefire trees, saplings, and seedlings.

*Distance to seed source.* We simulated stands at distances of 50 m, 500 m and 1 km from the nearest unburned seed source which could either represent forest at the fire edge or islands of unburned forest in the middle of burned patches. In actual fires, distance to seed source is primarily a function of the size and shape of high-severity burned patches. Seed supply and dispersal were modeled with species-specific negative exponential dispersal kernels and compared with field surveys (Appendix S1, S2).

*Variation in climate.* Effects of climate were simulated by driving the model with climate from three 30-year periods. We used a historical period (1950 to 1980) and two levels of climate change that represented a temperature increase of 3 and 5.5 °C, indicative of mid-century (2029-2059) and late-century (2069-2099) warming under the Representative Concentration Pathway (RCP) 8.5. The RCP 8.5 scenario represents a substantial increase in CO<sub>2</sub> over the next 100 years, although current trends suggest this emissions scenario is already being exceeded (Smith et al. 2016). We used the CNRM-CM5 global circulation model (GCM) (Voldoire et al. 2013), which reproduces historical conditions in the northern Rockies well (Westerling et al. 2011). Climate variables that

drive iLand simulations include maximum and minimum daily temperature, daily precipitation, radiation, and vapor pressure deficit. Climate data were statistically downscaled to a 4-km resolution using the Multivariate Adaptive Constructed Analogs approach (Abatzoglou and Brown 2012) (URL: <http://maca.northwestknowledge.net/index.php>). Data were extracted for one grid cell per elevation that corresponded to a median density field plot. We chose only one grid cell per elevation because we were not attempting to characterize effects of climate variation within elevation bands, but rather across the elevational range of the species' current distributions.

*Replication.* Simulations were each run 20 times and years were drawn randomly with replacement from the appropriate 30-year climate record to ensure the order of the climate record did not influence simulation results. This led to 20 replicates of each forest type (3 levels), substrate (2 levels), elevation (3 levels), FRI (4 levels), distance to seed source (3 levels) and climate (3 levels) combination.

#### *Model outputs*

We focused on two model outputs: frequency of regeneration failure at 30 years postfire (Question 1) and, if regeneration was successful during the historical climate period, the difference in mean tree density between historical and projected 21<sup>st</sup>-century climate (Question 2). Regeneration failure was defined as stands that had < 50 stems ha<sup>-1</sup> (including seedlings, saplings, and young trees) at postfire-year 30, which would indicate potential transition to a non-forest condition. The United Nations Food and Agricultural Organization (FAO) defines forest as any area > 0.5 ha that has > 10% canopy cover

(Chazdon et al. 2016). Our threshold of 50 stems  $\text{ha}^{-1}$  in Yellowstone would fall well below the FAO definition, and such densities are considerably lower than those commonly observed following recent fires in Yellowstone. For example, only 1.4% of early postfire (24 year) stands had densities  $< 50$  stems  $\text{ha}^{-1}$  after the 1988 Yellowstone fires (Turner et al. 2016). We then calculated the frequency of regeneration failure across the 20 replicates of each simulation. If regeneration was successful (i.e.,  $> 50$  trees  $\text{ha}^{-1}$ ) during the historical climate period, we calculated the difference in mean 30-yr postfire stem density between the historical and each projected 21<sup>st</sup>-century climate period.

### *Data analysis*

To address Question 1 (regeneration frequency), we first used ANOVA to explain factors influencing the frequency of regeneration failure based on the levels of each treatment in the simulation experiment. We conducted analyses separately by forest type. We then explored the influences of climate in more detail, applying linear mixed-effects models (LMMs). We included mean growing-season temperature, mean annual precipitation, mean growing season soil water potential, and number of growing season frost events as fixed-effects. Random effects included non-climate related treatment-level variables (i.e., distance to seed source and fire return interval). This approach allowed us to ask, controlling for non-climate related factors, what specific climate variables explained variation in response variables? We used the lme4 package in R (Bates et al. 2015) and all explanatory variables were assessed for collinearity. Variables were not included in the same model if they had a pairwise correlation of greater than 0.7. The dependent variable was transformed using a logit transformation. In regressions, all

continuous variables were standardized prior to analysis. Exhaustive model selection (Burnham and Anderson 2002) was conducted in all analyses (ANOVA and LMM) to determine the most important variables using the R package MuMIn (Barton, 2015). Top models ( $AIC_c < 2$ ) are presented for ANOVA and model-averages are presented for LMMs. Analyses were conducted in R statistical software (R Core Team 2016).

To address Question 2 (density differences), we first used ANOVA to explain differences in stand densities between the 21<sup>st</sup> century and historical periods, when regeneration was successful, for each forest type. We then used LMMs to identify climate variables that explained treatment level effects (as described above). A  $\sqrt[3]{\phantom{x}}$  transformation was applied to the dependent variable for serotinous lodgepole pine so that residuals were approximately normally distributed. All statistical analyses were conducted to efficiently find patterns in the simulated data as opposed to determine statistical significance. Thus, in results the magnitudes of difference between treatments are emphasized. In the text, means  $\pm$  one stand error are presented.

## RESULTS

Across all simulations, Douglas-fir densities at postfire year 30 ranged from 0 to 21,186 stems  $ha^{-1}$  (mean =  $2,677 \pm 327$  stems  $ha^{-1}$ , median = 132 stems  $ha^{-1}$ ). Non-serotinous lodgepole pine densities ranged from 3 to 3,197 stems  $ha^{-1}$  (mean =  $815 \pm 62$  stems  $ha^{-1}$ , median = 412 stems  $ha^{-1}$ ). Serotinous lodgepole pine densities were between 7 and 93,972 stems  $ha^{-1}$  (mean =  $23,120 \pm 1,730$  stems  $ha^{-1}$ , median = 4,569 stems  $ha^{-1}$ ). Simulated stand densities of these forest types closely matched field observations of postfire densities in Yellowstone (Donato et al. 2016, Turner et al. 2016) (Appendix S2).

In general, simulated densities decreased with distance to seed source and increased or stayed the same under 21<sup>st</sup> century climate, compared with historical conditions.

*Frequency of regeneration failure (Question 1)*

*Douglas-fir.* Douglas-fir failed to regenerate by postfire-year 30 in 55% of the simulations (Fig. 1), primarily due to distance from seed source (Table 2A, Fig. 2A). Regeneration was always successful if stands were 50 m from a seed source and nearly always failed when stands were 1 km away (Fig. 3A). Climate period was also an important driver, with regeneration failure declining from  $64 \pm 6\%$  under historical climate to  $41 \pm 5\%$  under late-21<sup>st</sup> century climate. When direct measures of climate were substituted for categorical variables, LMMs revealed that reduced failure of Douglas-fir regeneration in 21<sup>st</sup>-century climate periods was driven by fewer growing season frost events (Table 3A).

*Non-serotinous lodgepole pine.* Non-serotinous lodgepole-pine failed to regenerate by postfire-year 30 in 28% of simulations (Fig. 1). Like Douglas-fir, regeneration failure was most strongly determined by distance to seed source (Table 2A, Fig. 2B); failure was likely when stands were 1 km from a seed source and minimal when stands were 50 or 500 m away (Fig. 3B). Elevation and substrate had small effects on regeneration failure. Regeneration failure occurred more frequently at low (32%) versus high elevations (23%) and on rhyolite (29%) versus andesite substrate (26%). Climate period did not affect regeneration failure. LMMs revealed that the small effects of elevation and substrate reflected tradeoffs between drying soils, which increased

regeneration failure, and reduced growing season frost events, which decreased regeneration failure (Table 3A).

*Serotinous lodgepole pine.* Serotinous lodgepole pine failed to regenerate by postfire-year 30 in < 20% of simulations (Fig. 1). Regeneration failure was driven by distance to seed source, FRI, and their interaction (Table 2A, Fig. 2C). Regeneration failure was more frequent when stands were 1 km from seed source and FRIs were  $\leq 20$  years (Fig. 3C). As with non-serotinous lodgepole pine, elevation had a small effect on regeneration failure (19% at low versus 13% at high elevation), and climate period was unimportant (Table 3B).

#### *Density differences (Question 2)*

*Douglas-fir.* Where regeneration was successful under historical climate, simulated regeneration density in postfire-year 30 averaged  $1,205 \pm 114$  stems  $\text{ha}^{-1}$ . Postfire regeneration density increased nearly four fold (to  $4,036 \pm 411$  stems  $\text{ha}^{-1}$ ) under mid 21<sup>st</sup>-century conditions and six fold (to  $7,893 \pm 776$  stems  $\text{ha}^{-1}$ ) under late 21<sup>st</sup>-century conditions (Table 2B). Tree density increased only when stands were near (50 m) a seed source (Table 2B). Substrate also had a minor effect on density differences (Table 2B). LMMs revealed that stand densities increased with warming temperature and more precipitation (Table 3B, Fig. 4).

*Non-serotinous lodgepole pine.* Simulated stand densities averaged  $800 \pm 105$  stems  $\text{ha}^{-1}$  in stands where regeneration was successful under historical conditions and changed little in mid ( $910 \pm 116$  stems  $\text{ha}^{-1}$ ) and late ( $790 \pm 71$  stems  $\text{ha}^{-1}$ ) 21<sup>st</sup>-century periods (Table 2B). Densities were also slightly greater at low elevations close to seed



source (increasing to  $971 \pm 32$  stems  $\text{ha}^{-1}$ ) (Table 2B) but did not change at mid or high elevations. LMMs suggest decreases in annual precipitation and drying soils explained variability in stand density differences (Table 3B).

*Serotinous lodgepole pine.* When regeneration was successful, simulated densities of serotinous lodgepole pine at postfire year 30 averaged  $19,800 \pm 1,929$  stems  $\text{ha}^{-1}$  under historical conditions. Serotinous lodgepole pine densities increased by nearly 63% (by  $12,505 \pm 2,123$  stems  $\text{ha}^{-1}$  to reach  $> 32,000$  stems  $\text{ha}^{-1}$ ) at low elevations during 21<sup>st</sup>-century periods (Table 2B). Stand densities increased with a FRI of 50 years (to  $31,247 \pm 1,298$  stems  $\text{ha}^{-1}$ ) or 100 years (to  $26,013 \pm 1,566$  stems  $\text{ha}^{-1}$ ) (Table 2B). Distance to seed source had a modest effect as well, with densities increasing to  $27,900 \pm 1,927$  stems  $\text{ha}^{-1}$  at distances within 500 m of a seed source (Table 2B). Treatment level effects were explained by decreasing annual precipitation in the LMMs (Table 3B).

## DISCUSSION

Results of this study indicate that regeneration of two conifers following stand-replacing fire in subalpine forests is shaped by the complex interplay among several drivers related to future climate and fire regimes, some that constrain regeneration and others that enhance it. Overall, postfire regeneration of Douglas-fir and lodgepole pine was surprisingly resilient to the substantial changes in climate and fire regimes projected for Yellowstone, particularly when drivers were considered individually. Simulated regeneration failure generally required multiple changing drivers (Fig. 2). Stand-level simulation experiments cannot predict how and where forests will change across the landscape, and results could differ in mixed-species stands. However, this study reveals

complex responses to multiple changing drivers and offers insights into the mechanisms underpinning forest resilience (Trumbore et al. 2015, Reyer et al. 2015).

*What causes regeneration failure (or success?)*

Distance to seed source explained nearly all variation in regeneration failure for Douglas-fir and non-serotinous lodgepole pine, consistent with our hypotheses (Table 1). This finding suggests there are large consequences associated with projections of increased area burned during the 21<sup>st</sup> century (Westerling et al. 2011), as the size and shape of high-severity burn patches strongly determines regeneration of conifers that lack a canopy seed bank. Indeed, most regeneration following recent fires in the northern Rocky Mountains has occurred within 150 m of the unburned edge (Kemp et al. 2016, Donato et al. 2016, Harvey et al. 2016a). Our findings are consistent with prior studies that emphasize the importance of biotic residuals (i.e., propagules or surviving trees within large disturbed patches) for regeneration following large, infrequent disturbances (Turner et al. 1994, 1998, Franklin and Forman et al. 1987, Franklin et al. 2002, Seidl et al. 2014, Johnstone et al. 2016, Tepley et al. 2017).

Regeneration failure was uncommon in serotinous lodgepole pine stands, which develop canopy seedbanks. Regeneration failure only occurred in stands far from seed source when fires burned again before the development of the canopy seed source (Fig. 2). Serotiny is an effective fire adaptation expressed in a variety of species globally (Lamont et al. 1991, He et al. 2012). Dense seed rain from cones that open after fire enables serotinous tree species to establish rapidly in postfire environments where a flush of resources is available and competition is low (Tinker et al. 1994, Keeley et al. 2005,

Causley et al. 2016). Serotiny may also buffer against other drivers of postfire regeneration failure, including poor substrates for establishment (Johnstone and Chapin 2006, Johnstone et al. 2009), seed predation (Lamont et al. 1991; though see Benkman and Siepielski 2004), and postfire drought (Lamont and He 2017). This prolific production of seed may partly explain the lack of sensitivity to climate conditions in our simulation study. After the 1988 Yellowstone fires, postfire regeneration density in stands where prefire serotiny was high commonly exceeded 100,000 stems ha<sup>-1</sup>. Even if hostile conditions reduce stand density by 90% a robust forest will grow back. Serotiny can be an effective bet hedging strategy for species facing variable environments (Buma et al. 2013).

Serotinous stands lose their advantage if fires reoccur before trees are reproductively mature (Buma et al. 2013, Johnstone and Chapin 2006). Thus, postfire densities of serotinous species could be substantially reduced by short-interval fires, consistent with other systems where fire intervals are shortening (Keeley et al. 1999, Enright et al. 2015, Bowman et al. 2016). For example, serotinous black spruce (*Picea mariana*) seed supply was reduced 90% after short-interval fires in the Yukon Territories, Canada (Brown and Johnstone 2012). However, short FRIs alone were insufficient to initiate regeneration failure of simulated serotinous lodgepole pine stands in Yellowstone; burned stands also had to be far from seed source, limiting the seed supply from neighboring unburned stands.

Climate effects on regeneration failure differed by forest type. Warming enhanced Douglas-fir regeneration because frost events became less frequent during the growing

season. Although growing season frost became rare in simulations under 21<sup>st</sup>-century conditions, warming could expose seedlings to winter frost damage if snow cover is reduced because snow insulates seedlings from temperature fluctuations (Batllori et al. 2009, Renard et al. 2016). Reductions in winter snowpack are projected to be greatest at mid elevations in Yellowstone versus high elevations, where snowpack is projected to remain consistent (Tercek and Rodman 2016), or low elevations, where snow pack is already less. Winter warming could also delay sapling spring growth initiation if chilling requirements are no longer met (Ford et al. 2016). The insulating effect of snow and winter chilling is not currently represented in iLand, and further study is needed to determine how winter climate change may counter effects of declining growing season frost.

Our study suggests substantial resilience of lodgepole pine stands to projected warming; non-forest states rarely occurred in the simulation with the combinations of factors considered here, although tree density could change substantially in the future (e.g., Schoennagel et al. 2006). In part, this may reflect our conservative definition of regeneration failure ( $< 50$  stems  $\text{ha}^{-1}$  at postfire year 30) relative to the prolific regeneration capacity of lodgepole pine and its ability to produce cones at a young age (Turner et al. 2007). Our results are relatively consistent with climate suitability projections of 21<sup>st</sup>-century lodgepole pine and Douglas-fir distributions in Yellowstone, which suggest range reductions and distributional shifts to higher elevations. (Bartlein et al. 1997, Crookston et al. 2010, Coops and Waring 2011, Gray and Hamann 2013, Bell et al. 2014, Hansen and Phillips 2015). While our approach takes a step beyond climate

suitability studies by considering the processes that are important during a sensitive life-history stage (regeneration), we still only consider the responses of individual tree species to changing climate and fire. However, the abundance and distribution of a species can be strongly shaped by competitive interactions, particularly at local to landscape scales (Copenhaver-Parry et al. 2017), and process-based models are a promising tool for determining where and why interspecific biotic interactions might modulate how tree species respond to climate change.

*What explains changing stand densities?*

Postfire stand densities for all three forest types were sensitive to both fire and climate drivers, with fire frequency and size influencing potential establishment and climate conditions largely affecting survival and growth. As hypothesized, warming led to increased density of Douglas-fir in our simulations, particularly when precipitation also increased (Fig. 4). Densification of Douglas-fir regeneration under warmer climate is consistent with expectations for a tree species at the leading edge of its distribution (Hansen and Phillips 2015) and with the fossil pollen record in Yellowstone. Conditions were warmer than present during the early to mid Holocene, and Douglas-fir expanded to higher elevations—but only on andesite substrate (Whitlock 1993). The lack of edaphic constraints on Douglas-fir regeneration in our simulations suggests other factors (e.g., competition among tree species) may have shaped Douglas-fir distributions in response to past climate variation.

Postfire lodgepole pine stand density was influenced by multiple climate factors, acting in opposing directions. Decreasing annual precipitation, which mainly falls as

snow in Yellowstone, increased lodgepole pine densities. Reduced spring snowpack can lead to increased early postfire densities of tree species by lengthening growing seasons (Hansen et al. 2016), when there is sufficient soil moisture and little frost damage. However, soil drying decreased non-serotinous lodgepole pine densities. Effects of soil drying on lodgepole pine seedlings are well documented. Stand densities were substantially reduced in the northern Rockies when recent fires were followed by hot-dry versus cool-wet conditions (Harvey et al. 2016a). Disentangling effects of opposing climate drivers of postfire regeneration could be explored more fully with experimental approaches.

Considered together, our simulations of postfire regeneration suggest that forest-landscape patterns could become increasingly coarse-grained in the future, as climate changes and fires become larger and more frequent. The number and size of non-forest patches could increase, due to regeneration failure, but the surrounding forests may actually become more dense. This could have important consequences for forest susceptibility to subsequent disturbance agents (Seidl et al. 2016a) and the provision of ecosystem services (Turner et al. 2013, Spies et al. 2017). Changes in spatial patterns of forest cover and structure could also be sensitive indicators of forest resilience (Scheffer et al. 2012, Ghazoul et al. 2015, Seidl et al. 2016b). Increased regeneration failure over multiple fire cycles or shifting spatial patterns can indicate slowing of ecosystem recovery and impending transitions to alternate states (Kéfi et al. 2007, Dakos et al. 2011, Ghazoul and Chazdon 2017, Walker et al. 2016). Establishing resilience indicators for forest systems is particularly important because forests can respond slowly to drivers, and

marginal changes may go unrecognized if postfire recovery dynamics are not monitored through time (Hughes et al. 2013, Paine et al. 1998, Lindenmayer et al. 2016).

### *Conclusions*

Tree regeneration is a resilience linchpin in forests where large high-severity disturbances occur (Gauthier et al. 2015, Johnstone et al. 2016, Turetsky et al. 2017). Simulated postfire regeneration of two widespread subalpine conifers was surprisingly resilient to future climate and fire regimes. Multiple drivers were often required for regeneration to fail – distance to seed source, paired with cold temperature for Douglas-fir or with short FRIs for serotinous lodgepole pine (Fig. 2) – and such relationships may well apply to other obligate seeders. It appears that the indirect effects of 21<sup>st</sup>-century warming, causing an increase in the size and frequency of stand-replacing fire (Westerling et al. 2011, Harvey et al. 2016b), could exceed the direct effects of warming on early postfire conifer regeneration in Yellowstone.

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## TABLES

Table 1. Hypotheses of how changing climate and fire regimes will interact to cause postfire regeneration failure in subalpine forest types found throughout western North America (adapted from Johnstone et al. 2016).

Process	Driver	Hypothesized mechanism	Citations
Seed supply	Fire return interval	If fires become more frequent and sequential fires occur before trees mature, then postfire regeneration will be constrained. Serotinous lodgepole pine may be particularly vulnerable due to reliance on an <i>in situ</i> seedbank.	Buma et al. 2013
Seed delivery	Distance to seed source	If patches of stand-replacing fire exceed seed dispersal distances, postfire regeneration may be constrained, especially in the middle of large burned patches. Non-serotinous lodgepole and Douglas-fir may be particularly vulnerable due to their reliance on unburned trees as a seed source.	Harvey et al. 2016a, Turner et al. 1999, 2004, 2016
Seedling establishment	Postfire drought	If drought occurs in the first few years postfire, seedling establishment may be reduced even if seed is abundant. Lower montane sites, which are already warmer and drier, may be especially vulnerable to drought.	Harvey et al. 2016a



Table 2. ANOVA results of top models ( $AIC_c < 2$ ) predicting A. frequency of regeneration failure and B. density differences between 21<sup>st</sup>-century and historical periods, if regeneration was successful. Regeneration failure frequency was logit transformed. Density differences for serotinous lodgepole pine was transformed to the  $\sqrt[9]{}$ . Sum of squares, F-values, significance levels and model adjusted  $R^2$  are presented.

	Douglas-fir			Non-serotinous lodgepole pine	Serotinous Lodgepole pine
	Model 1	Model 2	Model 3	Model 1	Model 1
<b>A. Regeneration failure</b>					
Distance to seed source	3,843.8***	3,877.9***	3,846.9***	2,503.4***	519.0***
	2,634.9	2,634.9	2,634.9	1,868.7	667.7
Climate Period	165.8***	167.3***	165.9***		
	113.7	113.7	113.7		
FRI					68.1***
					131.4
Elevation		1.9		41.4***	16.8***
		1.3		30.9	21.6
Substrate			1.2	16.3***	
			0.4	6.1	
Distance x Climate period	58.3***	58.8***	58.3***		
	79.9	79.9	79.9		
Distance x FRI					61.9***
					238.9
Distance x Elevation				16.3***	
				24.3	

Adj. R <sup>2</sup>	0.97	0.97	0.97	0.96	0.88
<b>B. Density differences</b>					
Distance to seed source	1,225.6***			28.0***	30.8***
	1.7x10 <sup>9</sup>			1.1x10 <sup>6</sup>	94.5
Climate Period	192.9***			27.1***	
	2.7x10 <sup>8</sup>			5.1x10 <sup>5</sup>	
FRI					31.1***
					142.9
Elevation				24.2***	57.3***
				9.1x10 <sup>5</sup>	175.6
Substrate	22.4***				
	3.2x10 <sup>7</sup>				
Distance x Climate	176.8***				
period	2.5x10 <sup>8</sup>				
Elevation x FRI					14.4***
					132.9
Distance x Elevation				17.5***	
				1.3x10 <sup>6</sup>	
Adj. R <sup>2</sup>	0.95			0.58	0.71

---

\*p<0.05, \*\*p<0.01, \*\*\*p<0.001

Table 3. Averaged Linear mixed effects regression results of top models (AICc &lt; 2) predicting

A. frequency of regeneration failure and B. density differences between 21<sup>st</sup> century and

historical periods, if regeneration was successful. Regeneration failure frequency was logit

transformed. Density differences for serotinous lodgepole pine was transformed to the  $\sqrt[3]{\phantom{x}}$ .

Coefficients of all continuous variables were standardized to z-scores and significance levels are

presented for fixed effects. Standard deviations are presented for random effects

	Douglas-fir	Non-serotinous lodgepole pine	Serotinous lodgepole pine
<b>A. Regeneration failure</b>			
<i>Fixed effects</i>			
Intercept	0.02	-0.003	-0.004
Growing season frost events	0.16***	0.09**	0.14**
Growing season soil water potential		-0.11***	-0.04
Growing season temperature	-0.06**		
Annual precipitation		-0.01	-0.04
Frost events x temperature	0.03		
Frost events x soil water potential			-0.03
Frost events x Precipitation		-0.006	-0.02
<i>Random effects</i>			
FRI			0.37
Distance to seed source	0.95	0.96	0.76
<b>B. Density differences</b>			
<i>Fixed effects</i>			
Intercept	-0.16	0.14	0.06
Growing season frost events		0.14	0.07

Growing season soil water potential		0.30**	-0.01
Growing season temperature	0.47***		
Annual precipitation	0.41***	-0.54***	-0.41***
Precipitation: Temperature	-0.14*		
Frost events: Precipitation		0.22**	0.07
Frost events: soil water potential			0.04
Precipitation: soil water potential			-0.02
<i>Random effects</i>			
FRI		0.26	0.45
Distance to seed source	0.83	0.37	0.38

---

\*p<0.05, \*\*p<0.01, \*\*\*p<0.001

## FIGURE LEGENDS

**Figure 1.** Frequency of regeneration failure (%) at postfire-year 30 for Douglas-fir (DF), non-serotinous lodgepole pine (LP-NS) and serotinous lodgepole pine (LP-S) across all simulations. Values are means  $\pm$  2 standard errors.

**Figure 2.** State space conceptually summarizing conditions that led to postfire-year 30 tree regeneration failure and success as a function of distance to seed source, fire return interval, and climate period for (A) Douglas-fir, (B) non-serotinous lodgepole pine, (C) serotinous lodgepole pine, three widespread forest types in Rocky Mountain forests.

**Figure 3.** Frequency of regeneration failure (%) at postfire-year 30 as a function of distance from seed source and fire return interval (FRI) for (A) Douglas-fir, (B) non-serotinous lodgepole pine, (C) serotinous lodgepole pine. Values are means  $\pm$  2 standard errors.

**Figure 4.** Differences in early postfire (30 year) Douglas-fir stand density between historical and 21<sup>st</sup>-century climate periods versus 21<sup>st</sup> century annual precipitation (mm) and growing season mean temperature (°C). Values are predictions from a loess fit.

## FIGURES

Figure 1.

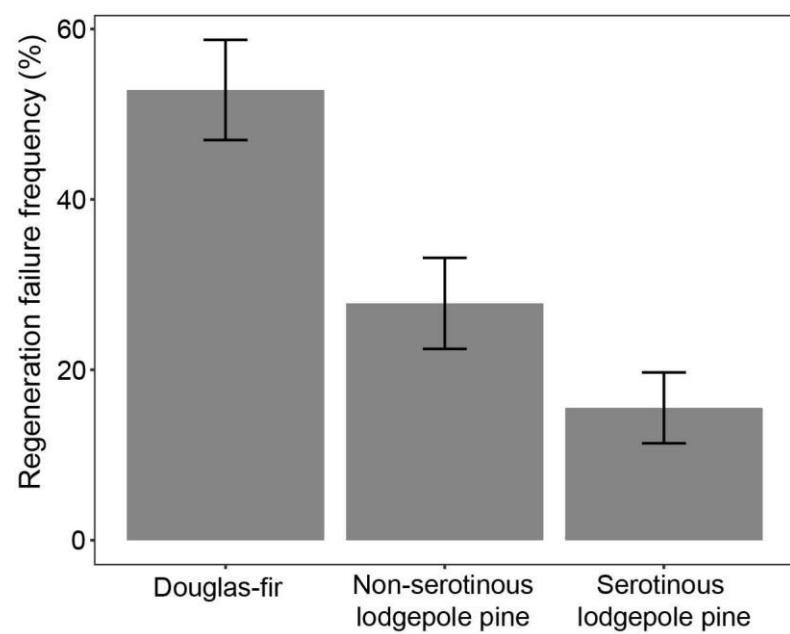


Figure 2.

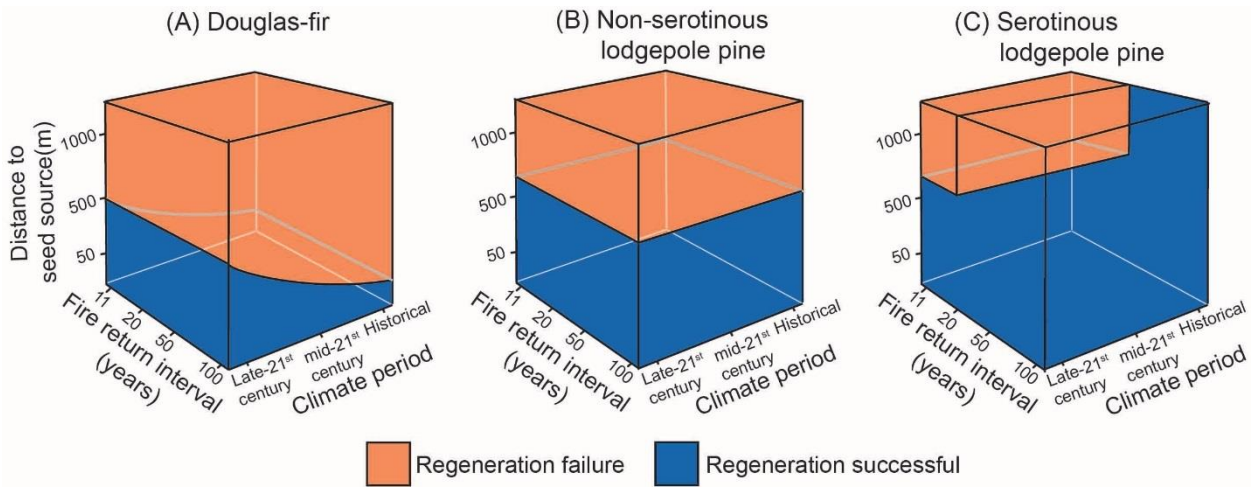


Figure 3.

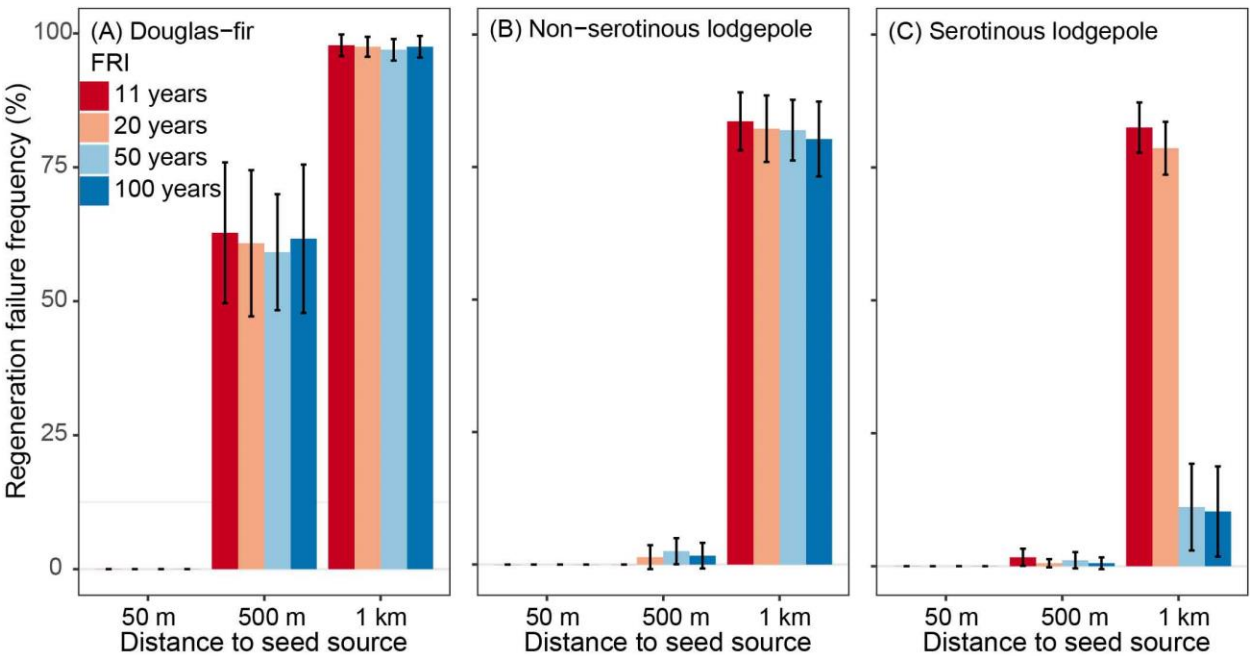
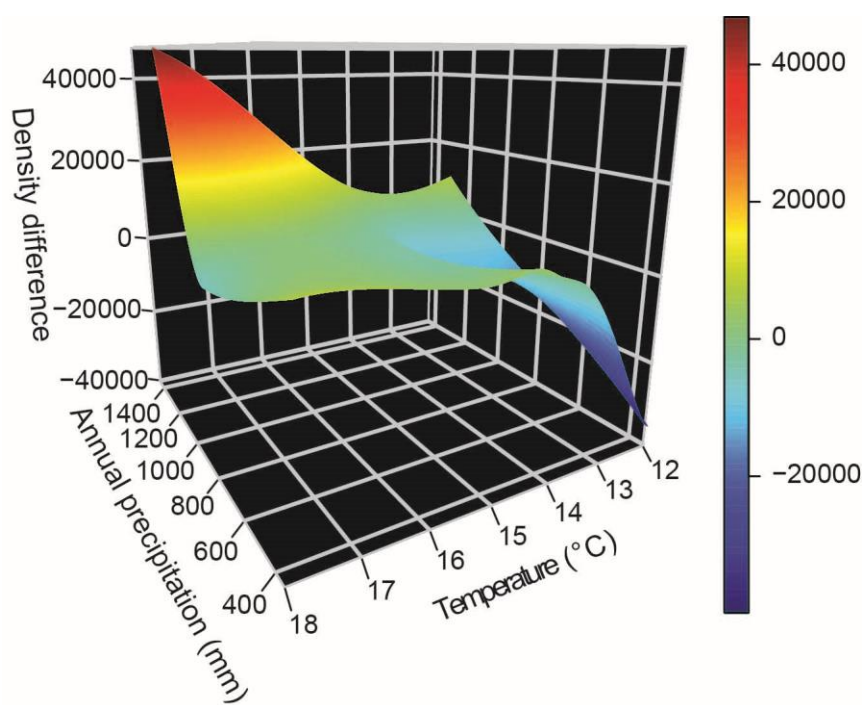




Figure 4.



## SUPPLEMENTAL MATERIAL

**Appendix S1**

**Table S1.** iLand regeneration module parameters used to explore effects of changing fire regimes and postfire warming/drying on tree regeneration of and Douglas-fir (DF), non-serotinous lodgepole pine (LP-NS), and serotinous lodgepole pine (LP-S) stands in Yellowstone National Park, Wyoming, USA. Extensive model documentation is available at (<http://iland.boku.ac.at/iLand+Hub>).

Parameter name	Units	Source	LP-NS	LP-S	DF
<i>Seed production/ dispersal</i>					
Cone bearing age	years	8, 10, 12-13	15	15	55
Seed year interval	years	9, 10, 12; 14-19	1	1	5
Non- seed year fraction	dim[0,1]	9, 10, 12; 14-19	0	0	0.24
Seed mass	mg	10, 11, 12,	4.1	4.1	11.31
Germination rate	dim[0,1]	49, 20-24	0.36	0.36	0.30
Fecundity	sdlings m <sup>-2</sup>	24-25	115.9	115.9	43.9
Seed kernel a	m	10, 26-30	6	6	30
Seed kernel b	m	10, 26-30	160	160	200
Seed kernel c	dim[0,1]	1	0.05	0.05	0.2
<i>Establishment</i>					
Min temperature	°C	31	-85	-85	-37
Chill requirement	days	31	63	63	56
Min growing degree days	degree days	31	186	186	340
Max growing degree days	degree days	31	3374	3374	3261

Growing degree days base temperature	°C	31	2.9	2.9	3.4
Growing degree days bud burst	degree days	31	116	116	255
Frost free days	days	31	80	80	100
Frost tolerance	dim[0,1]	31	0.9	0.9	0.5
Min soil water potential	MPa	31	-2.3	-2.3	-7
<i>Sapling growth</i>					
Sapling growth a	dim	2,3-7, 32-41	0.05	0.05	0.036
Sapling growth b	m	2,3-7, 32-41	24	24	47
Max number of years under stress	years	This paper	2	2	3
Stress threshold	dim[0,1]	34	0.2	0.2	0.05
Height to diameter ratio	dim	2, 3, 5, 7	72	72	88
Reineke's R	saplings ha <sup>-1</sup>	2, 3, 5, 7, 34	14.33	550	500
Reference ratio	dim[0,1]	This paper	0.457	0.457	0.451
<i>Serotiny</i>					
Serotiny formula	dim[0,1]	3	x,20,0,80,1		
Serotiny fecundity		3	30		

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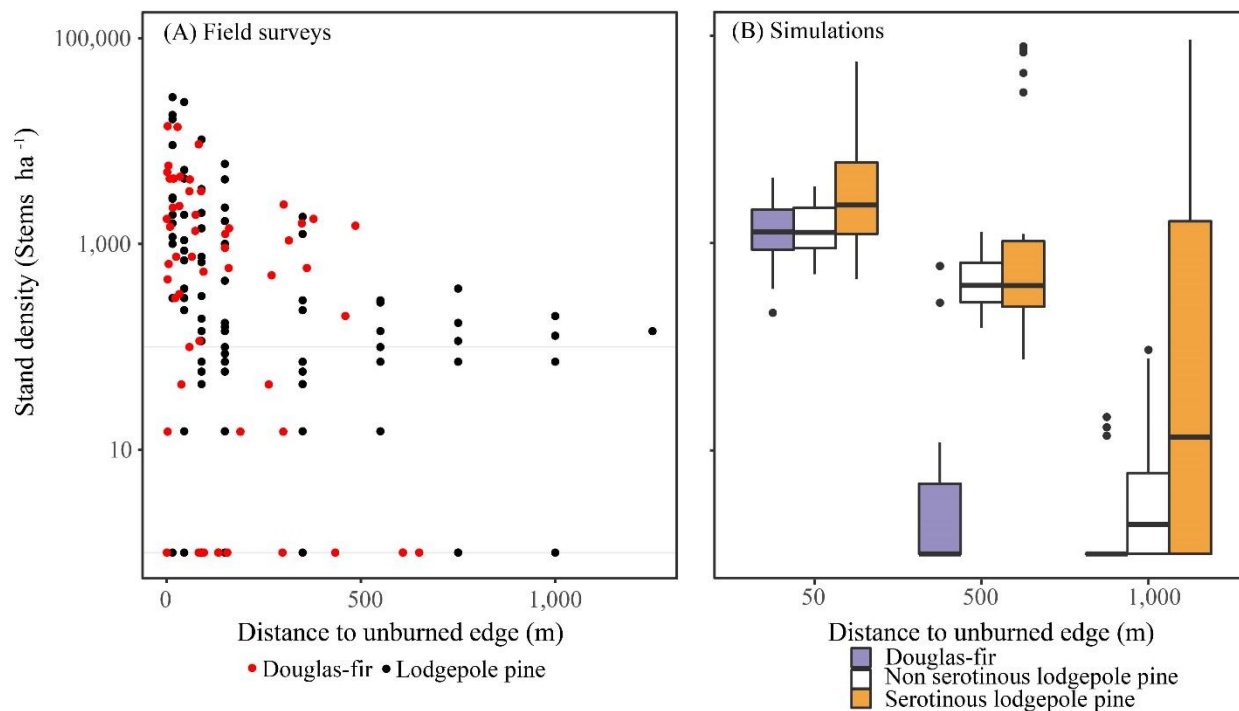
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## Appendix S2.

We evaluated how well iLand simulated variation in early postfire lodgepole pine and Douglas-fir densities as a function of distance to seed source based on species specific dispersal kernels (Table S1). We compared simulated densities at 50 m, 500 m, and 1 km with early post fire stand densities measured in field surveys throughout Yellowstone. Stem densities from field surveys declined with distance to seed source and closely matched simulated densities (Fig. S1).

Douglas-fir densities declined more quickly than lodgepole-pine densities and no Douglas-fir seedlings established 1 km from seed source in either field surveys or simulations.

**Figure S1.** Early postfire densities of Douglas-fir and lodgepole pine stands as a function of distance to seed source in (A) field surveys after recent fires in greater Yellowstone (Harvey et al. 2016a, Donato et al. 2016), (B) simulations in iLand.



Running Head: Fire Suppression in Subalpine Forests

**Chapter 4 –Fire suppression in 21<sup>st</sup>-century subalpine forests of Greater Yellowstone**

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**Abstract**

Fire activity is rapidly increasing in subalpine forests of the western United States. Managers must make difficult decisions regarding the use of fire suppression under highly uncertain conditions. We used a process-based simulation model, iLand, to characterize how a contemporary subalpine-forest landscape in Greater Yellowstone would be different if fires had not been suppressed during the last three decades and how letting fires burn may affect 21<sup>st</sup>-century fire and forests. More area burned when fires were not suppressed, but neither 21<sup>st</sup>-century fire trends nor contemporary or future forests were meaningfully altered. Our results suggest managers have tremendous flexibility to strategically suppress 21<sup>st</sup>-century subalpine fire without worrying that current actions will affect subsequent fire extent or forest cover – unlike in dry conifer forests. Applying distinct nationally coordinated fire-management approaches across multiple forest types could result in more effective resource allocation during the large-fire era.

**Keywords:** *Climate change; Fire management; Forest resilience; Greater Yellowstone; Northern Rocky Mountains; Simulation; Subalpine forests; Wildfire*

## INTRODUCTION

Forests of western North America are in a large-wildfire era, at least partially because of human-caused climate change (Littell et al. 2009, Abatzoglou and Williams 2016). Warming and drying have produced large upticks in the frequency and size of forest fires by lengthening the season where burning occurs (Westerling et al. 2006, Kitzberger et al. 2017). Many western tree species are well adapted to fire (Romme 1982), and it is an essential ecosystem process (Romme et al. 2011). However, increased burning has coincided with expansion of the wildland urban interface (Radeloff et al. 2018), causing tremendous growth in costs of managing fire. Federal agencies spent more than 1 billion dollars on fire suppression in 14 of the last 17 years and almost 3 billion dollars in 2017 (National Interagency Fire Center 2017).

Wildfires in subalpine forests account for a large percentage of the increased burning (Westerling 2016). Subalpine fires are generally large ( $10^2$ -  $>10^5$  ha), infrequent (every 100-300yrs), severe (stand replacing) (Turner et al. 1994, Loehman et al. 2018), and climate limited (Bessie and Johnson 1995). Thus, subalpine fires are sensitive to climate change, and thresholds exist where a little warming causes huge increases in burning (Turner and Romme 1994, Westerling et al. 2006). Given 21<sup>st</sup>-century temperature projections, burned area is expected to continue growing rapidly in subalpine forests and may only slow if fuels become limiting (Westerling et al. 2011).

Projected climate-fire trends could exceed the resilience of subalpine forests, causing them to change fundamentally (Turner 2010). Wildfire can be a powerful catalyst of forest reorganization (Johnstone et al. 2016) because postfire seedling densities depend on seed supply and soil moisture (Hansen et al. 2018), and early tree regeneration sets the template for decades of succession (Kashian et al. 2005, Martínez-Vilalta and Lloret 2016). Already, seedling

densities have been substantially reduced when recent fires burned unusually large patches or were followed by drought. (Harvey et al. 2016a, Stevens-Rumann et al. 2017).

Fire managers must make difficult decisions regarding the uncertain future of subalpine forests (Schoennagel et al. 2017, Halofsky et al. 2018). Managers are effective at suppressing subalpine fires under average weather conditions, but large fires that burn under extreme weather are difficult to suppress (Keane et al. 2008). Congruent with rising suppression costs, federal policy is providing more flexibility to monitor or partially suppress fires, and these decisions could have lasting consequences. Twentieth-century observations suggest past fire exclusion in subalpine forests likely has not increased subsequent fire size or severity – in direct contrast to dry conifer forests (Schoennagel et al. 2004, Stephens et al. 2013). However, it is unclear whether past observations will accurately characterize suppression effects in subalpine forests during the large-fire era, particularly if fuel limitations grow or forest resilience erodes.

We used a process-based forest model, iLand (Seidl et al. 2012), to characterize how a contemporary subalpine-forest landscape in Greater Yellowstone (Fig. 1) would be different if fires had not been suppressed during the last three decades and how letting fires burn (vs. suppressing them) may affect 21<sup>st</sup>-century fire and forests. Greater Yellowstone is a massive intact ecosystem in the northern Rocky Mountains, dominated by subalpine lodgepole pine (*Pinus contorta* var. *latifolia*), with spruce-fir (*Picea engelmannii* and *Abies lasiocarpa*) at higher elevations. Sagebrush-grasslands transition to Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and pockets of trembling aspen (*Populus tremuloides*) at lower treeline (Despain 1990). Spring-summer temperature is expected to warm 4-5°C by 2100, and statistical climate-fire models (based on weather alone and assuming adequate fuel) project fire rotation (time to burn

an area equivalent to a landscape of interest) to decline from > 120yrs to < 20yrs (Westerling et al. 2011). Fuel limitations are almost certain to manifest before such short fire rotations are actually realized, but it is plausible that more burning occurs in coming decades than at any point in the last 10,000 years.

## METHODS

### *Model overview*

iLand simulates forests using a hierarchical framework, where broader-scale processes emerge dynamically from interactions among individual trees (Seidl et al. 2012) (online documentation: <http://iland.boku.ac.at>). Tree growth, mortality, and competition are modeled in response to canopy-light interception, radiation, temperature, soil water, and nutrients. Climate and soil are assumed spatially homogeneous within a 1-ha cell, but variation in light is simulated at 2×2m resolution based on forest structure. iLand is forced with daily temperature, precipitation, vapor pressure deficit, and radiation. iLand explicitly simulates tree-regeneration processes, such as seed production (including serotiny), dispersal, and environmental controls on seedling establishment (Hansen et al. 2018). In addition to sexual reproduction, iLand also represents re-sprouting for aspen.

iLand dynamically simulates wildfire in a framework designed for the northern Rocky Mountains (Keane et al. 2011) and western Oregon (Seidl et al. 2014) (Appendix 1). Fires ignite based on moisture and regional fire probability, given sufficient fuels. Moisture is represented by the Keetch-Byram Drought Index (KBDI), a daily metric combining temperature and precipitation (Keane et al. 2011, Seidl et al. 2014). A maximum fire size is then chosen from a negative exponential distribution. Fire size is strongly related to seasonal weather in subalpine

forests, so we extended the module to ensure only large fires (>225 ha) are chosen when there is drought, and smaller fires (< 40 ha) are chosen with wet conditions (Appendix 1). Fire is then spread at a 20-m resolution. Spread probability to adjacent pixels is determined by wind, topography, and fuels. Fuel constraints are set conservatively: a fire will not spread if < 6kg m<sup>2</sup> of biomass is present in neighboring pixels (Sikkink and Keane 2012, Nelson et al. 2016). Fuels are represented by litter and coarse-wood carbon pools. Fire severity is modeled as percent crown kill, based on fuels, moisture, and bark thickness.

### *Simulation experiment*

We first conducted a 300-yr spin-up under historical climate and fire to generate a simulation landscape that was representative of the actual landscape (Appendix 2). We then tested how letting fires burn (vs. suppressing them) from 1989-2099 under moderate weather would alter a contemporary forest landscape and affect 21<sup>st</sup>-century fire and forests.

*Climate.* Simulations were forced with climate from two general circulation models (GCMs) and 4.5 and 8.5 representative concentration pathways (RCPs). We used the CNRM-CM5 and GFDL-ESM2M GCMs, which represent historical conditions in Greater Yellowstone well (Westerling et al. 2011). They project ~ 5.5 and 4.5 °C of summer warming by 2099 under the 8.5 RCP.

*Fire suppression.* We simulated two management scenarios. In the first, fires that burned under moderate moisture conditions were suppressed (size = 0.04ha; fire-module cell size). Fires that ignited under drought conditions burned unhindered. In the second scenario, all fires burned naturally. Fire is stochastic in the model, so we conducted 20 replicate simulations of each GCM x RCP x management scenario ( $n = 160$ ).



*Uncertainty analysis*- Climate projections remain highly uncertain, and the uncertainty propagates through statistical climate-fire models. Thus, we exhaustively explored the plausible 21<sup>st</sup>-century climate-fire space by conducting an uncertainty analysis for fire size using the CNRM GCM (8.5 RCP). We increased the *minimum* fire size that ignites under drought conditions (normally 225ha) by 2 times, 3 times, or 5 times, further reducing fire rotation. Againb 20 replicates of each combination were run ( $n = 120$ ).

#### *Response variables and analysis*

We focused on area burned, number of fires, area-weighted mean burned patch size, percent of stockable area that was non-forested, stand age, and tree-species dominance in 2017. Response variables were calculated for the landscape. Area burned and number of fires were analyzed separately for small (< 10ha), medium (10-40ha), medium-large (40-100ha) and large (>225ha) fires. Non-forest was defined as any stockable 1-ha cell with < 50 trees, saplings, or seedlings (Hansen et al. 2018). Stand age was broken into young (< 40yrs), middle (40-150yrs), middle/old (150-250yrs) and old (>250yrs) classes. Species dominance was calculated with species importance values (0 to 2), the sum of relative density and relative basal area. We then evaluated how fire- and forest-response variables changed between 2017 and 2099 for baseline and uncertainty-analysis simulations.

*Analysis.* We quantified differences among scenarios by comparing means and bootstrapped 95% confidence intervals (CIs). Differences (among scenarios and over time) were considered significant if CIs did not overlap. However, biologically meaningful differences were emphasized.

## RESULTS

### *Q1 Contemporary landscape*

On average, six times more area burned cumulatively when fires were not suppressed between 1989 and 2017 (Fig. 2A). The fire rotation was ~160yrs in the no-suppression scenario and 1,150yrs in the suppression scenario. Nearly 65 times more moderate-sized (10-225ha) fires and twice as many large fires (>225ha) burned in the no-suppression scenario (Fig. 2B). Area-weighted mean burned patch size was 90ha in the no-suppression scenario and 22ha in the suppression scenario. Fire response variables did vary among GCMs and RCPs, but differences between suppression scenarios remained consistent.

Forests changed little, irrespective of fire suppression. Most stands were < 40yrs-old, and virtually all were < 150yrs-old (Fig. 2C), regardless of suppression scenario. Forested area was dominated by lodgepole pine (65%), with 20%, 14%, and 1% dominated by Douglas-fir, spruce-fir, and aspen (Fig. 2D). Seven percent of stockable area was non-forested in 2017.

### *Q2 21<sup>st</sup>-century fire and forests*

Cumulative burned area grew faster when fires were not suppressed during the 21<sup>st</sup> century (Fig. 3). By 2099, almost twice as much area had burned, and fire rotation had declined to ~80yrs (vs. 150yrs in the suppression scenario). The percentage of large fires also increased to 26% and 21% in the no-suppression and suppression scenarios, respectively, accounting for 80% and 97% of cumulative burned area. Concordantly, area-weighted mean burned patch size grew to almost 200ha and 150ha in the no-suppression and suppression scenarios.

Again, there were few differences in 21<sup>st</sup>-century forests if fire were or were not suppressed. Stand age always declined. By 2099, young stands (<40yrs-old) made up ~85% of forested area, irrespective of management scenario (Fig. 4A). Lodgepole pine dominance

declined markedly and was replaced by Douglas-fir (Fig. 4B). Spruce-fir and aspen dominance remained similar. Percent non-forest declined to ~6% in 2099.

In the uncertainty analysis of fire size, burned area grew more rapidly during the 21<sup>st</sup> century with increased minimum fire size than in baseline simulations, and differences in burned area between management scenarios diminished (Fig. 5A). In 2099, fire rotation was as short as 24yrs and 27yrs in the no-suppression and suppression scenarios. Climate-fire thresholds were crossed in the latter half of the 21<sup>st</sup> century where area burned grew non-linearly, regardless of management scenario (Fig. 5A). Climate-fire thresholds were not present in the baseline simulations when fire rotation was as short as 67yrs.

Non-linear increases in burned area initiated sharp increases in percent non-forest, irrespective of fire suppression (Fig. 5B). During the first half of the 21<sup>st</sup> century, percent non-forest declined to ~5% of stockable area. As climate-fire thresholds were crossed and burned area grew, percent non-forest increased abruptly, peaking at 12% to 35% of stockable area (Fig. 5B). Stand age further declined with additional burning, but species dominance was not affected.

## DISCUSSION

Our findings indicate that not suppressing subalpine fire increases area burned but does not meaningfully alter 21<sup>st</sup>-century fire trends and does not affect contemporary or future forest extent and dominant species, even under the most extreme fire activity projected in statistical climate-fire models. These results suggest there are opportunities to develop nuanced fire-management approaches by embracing differences among distinct fire regimes in the western US. There is currently a strong call to bolster forest resilience by restoring fire-adapted forests (North et al. 2015, Stephens et al. 2016, Parks et al. 2018a). This is an important priority in dry

conifer forests because fire exclusion leads to the accumulation of ladder fuels, which causes surface fire to transition to crown fire (Allen et al. 2002, Savage and Mast 2005). However, the approach is far less applicable when fires are climate limited, like in subalpine forests (Noss et al. 2006, Halofsky et al. 2018). Our results demonstrate how managers could have tremendous flexibility to strategically suppress 21<sup>st</sup>-century subalpine fire, given appropriate weather, without worrying that current actions will affect subsequent fire or forest landscapes. Applying distinct but nationally coordinated fire-management approaches across multiple forest types could lead to more effective use of limited resources during a time when fire activity is only likely to grow.

Why does suppression not influence 21<sup>st</sup>-century subalpine fire? Fuel buildup is an important mechanism through which suppression changes fire. Yet, fuels never became limiting in our simulations. Young subalpine forests accumulate fuels quickly (Nelson et al. 2016). Field surveys and simulations of 24yr-old lodgepole pine in Greater Yellowstone showed that fuels were sufficient to support crown fire spread in over 90% of stands under average moisture and wind conditions (Nelson et al. 2017). In fact, more than 18,000 ha of young forest (< 30yrs-old) burned in Greater Yellowstone during summer 2016. Past fire in subalpine forests reduces subsequent fire likelihood for some time (Parks et al. 2014, Harvey et al. 2016c, Prichard et al. 2017). However, the duration is shortened with hot-dry conditions (Parks et al. 2018b), and given climate projections, the short self-limiting capacity of subalpine fire will likely be further reduced.

Fire suppression had minimal impact on contemporary or future forests. Suppression did cause the fire rotation to increase from the historical average (i.e., fire deficit *sensu* Parks et al.

2015), but subalpine forests did not change as a result. This is unsurprising because historical variability in fire-free intervals has been substantial, and 300- to 400-yr periods between fires are common (Romme 1982, Schoennagel et al. 2008, Bradford et al. 2008). In our simulations, 21<sup>st</sup>-century forests were still far more likely to experience unusually frequent burning when fires were suppressed, rather than unusually long fire-free intervals. Lodgepole pine was replaced by drought tolerant Douglas-fir in places, but this occurred whether fires were suppressed or not.

Simulated subalpine forests proved remarkably resilient to changing climate and fire. We did identify 21<sup>st</sup>-century thresholds of burning where percent non-forest abruptly increased, but our simulated landscape remained largely forested. Burned patch size is an important determinant of postfire tree regeneration (Harvey et al. 2016a, Stevens-Rumann et al. 2017), and simulated fires may not have regularly exceeded the size threshold necessary to cause landscape-level reductions in postfire seed supply. The largest burned patch size in our simulations was ~1,600 ha. Much larger severely burned patches are not uncommon in subalpine forests (Harvey et al. 2016b), and fire size could continue to increase in the 21<sup>st</sup> century. However, subalpine forests are well adapted to high-severity fires (Romme 1982) and experienced substantial variation in climate and fire over the past 8,000yrs without changing qualitatively (Millspaugh et al. 2000, Power et al. 2011). We still poorly understand how much change subalpine forests can absorb (Turner 2010), but simulations indicate decisions regarding suppression of fire will probably have little influence on forest resilience.

## CONCLUSION

A fire-management approach tailored to subalpine forests could be valuable for 21<sup>st</sup>-century forest stewardship in the western US. Suppression of all fires is not feasible in subalpine

forests. However, managers could strategically suppress fires, given appropriate weather, to defend social-ecological values at risk. The need to protect people and homes will remain (Radeloff et al. 2018). There is also growing awareness that suppression could be applied to maintain ecological attributes (e.g., structural and functional heterogeneity) (Halofsky et al. 2018). The window for even strategic fire exclusion may be closing, though, as conditions become hotter and drier and more fires grow large, making them impossible to suppress. If increased fire activity in subalpine forests is inevitable, then social adaptation may be the only truly viable fire-management approach in the large-fire era (Schoennagel et al. 2017).

#### ACKNOWLEDGEMENTS

WDH and MGT designed the study, WR and RS provided model code, WDH ran simulations and WR consulted, WDH and MGT wrote the paper and all others contributed. The authors acknowledge Kristin Braziunas and Zak Ratajczak for helpful comments on simulations. This research was funded by a grant from the National Park Service, Alaska Climate Science Center, and the University of Wisconsin-Madison Vilas Trust. R. Seidl and W. Rammer acknowledge support from the Austrian Science Fund through START grant Y895-B25.

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## FIGURE CAPTIONS

**Figure 1.** Map of the simulation landscape in southern Greater Yellowstone. Initial forest types are shown.

**Figure 2.** (A) Cumulative area burned and (B) cumulative number of fires (1989-2017) in small (<10 ha), medium (10-100 ha), medium-large (100 – 225 ha), and large (>225 ha) fires. (C) Percent of forest landscape in young (< 40yrs), middle (40-150yrs), middle-old (150-250yrs) and old (>250yrs) stand-age classes and (D) Percent of forest landscape dominated by lodgepole-pine, Douglas-fir, spruce-fir and aspen in 2017. Data are broken out by GCM for the 8.5 RCP. Simulations with the 4.5 RCP showed similar trends. Values are means  $\pm$  95% confidence intervals from 20 replicate simulations.

**Figure 3.** Cumulative area burned from 2017-2099 in small (<10ha), medium (10-100ha), medium-large (100-225ha), and large (>225ha) fires in (A) no-suppression and (B) suppression scenarios. Data are broken out by GCM (CNRM or GFDL) for the 8.5 RCP. Simulations with the 4.5 RCP showed similar trends. Values are means from 20 replicate simulations.

**Figure 4.** Percent of forested landscape in (A) young (<40yrs), medium (40-150yrs), medium-old (150-250yrs) and old (>250yrs) stand age classes and (B) dominated by lodgepole-pine, Douglas-fir, spruce-fir and aspen between 2017-2099 for no-suppression and suppression scenarios. Data are broken out by GCM (CNRM or GFDL) for the 8.5 RCP. Simulations with the 4.5 RCP showed similar trends. Values are means from 20 replicate simulations.

**Figure 5.** (A) Cumulative area burned and (B) percent of stockable area that was non-forested between 1989-2099 in the uncertainty analysis where the *minimum* large fire size was increased two, three, or five times for the no-suppression and suppression scenarios. Uncertainty analysis simulations were only run from the CNRM GCM and the 8.5RCP. Values are means  $\pm$  95%

confidence intervals from 20 replicate simulations. Map insets show the probability (across the 20 replicates) of stockable cells being non-forested in 2099.

## FIGURES

Figure 1.

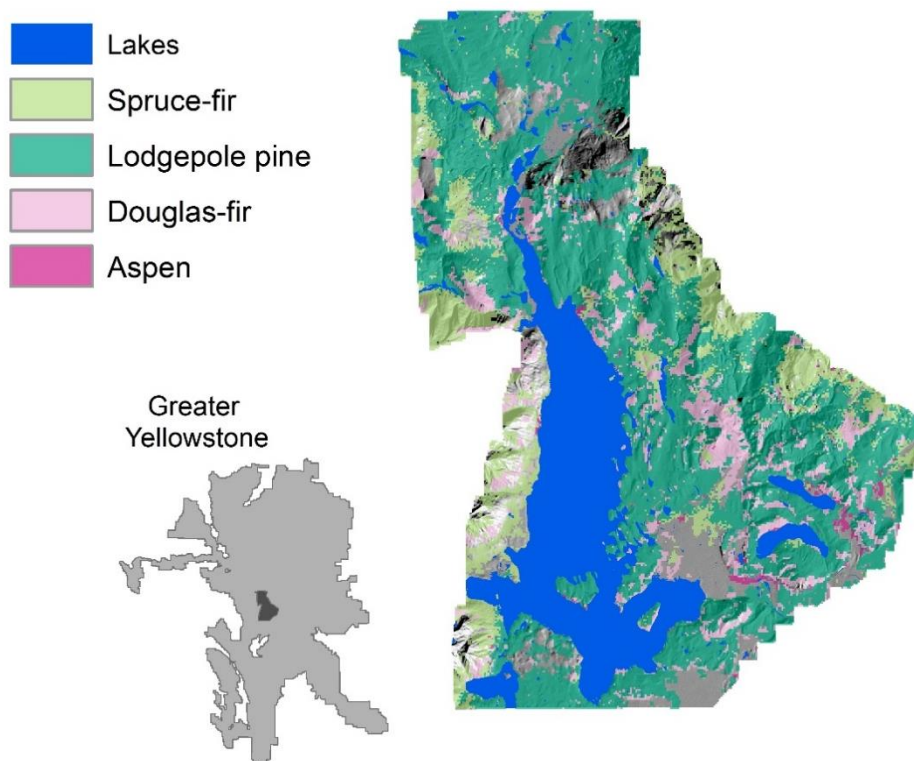




Figure 2.

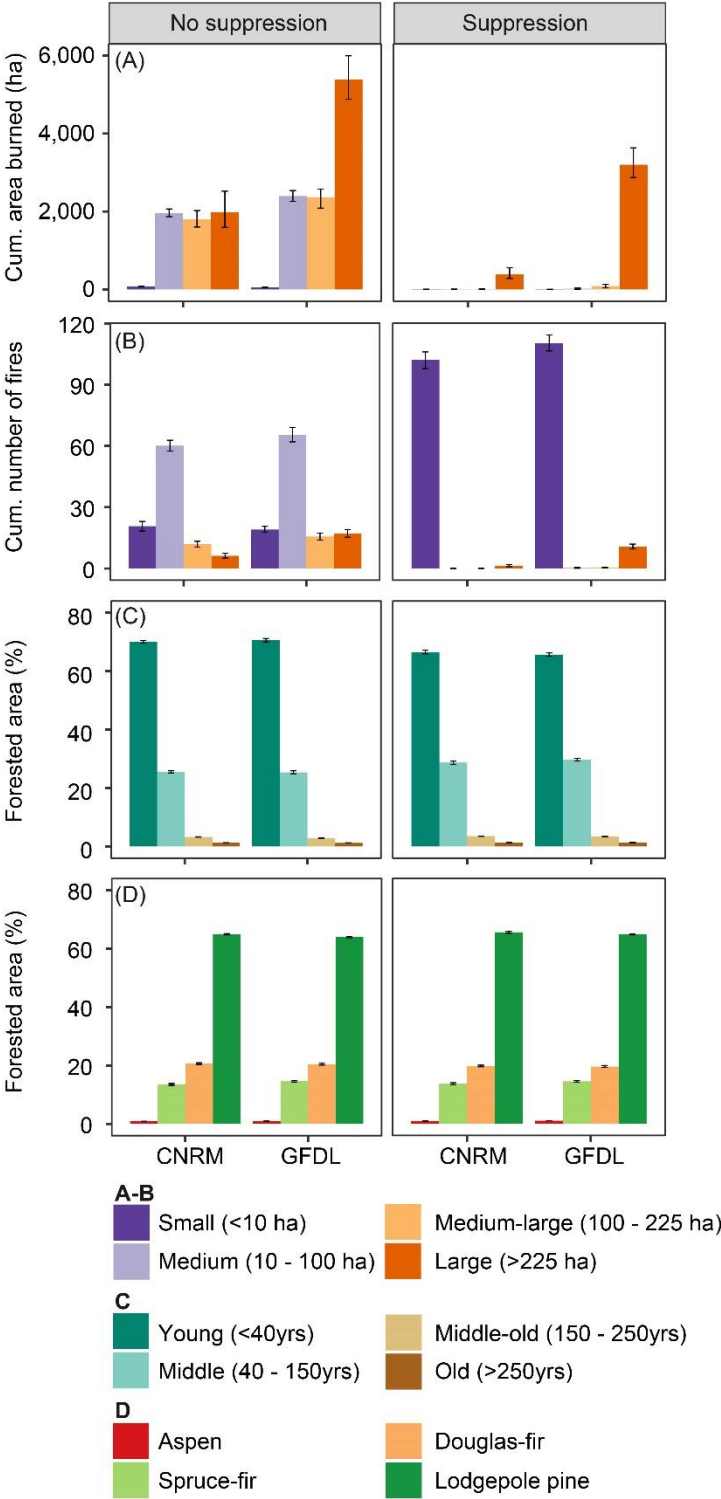


Figure 3.

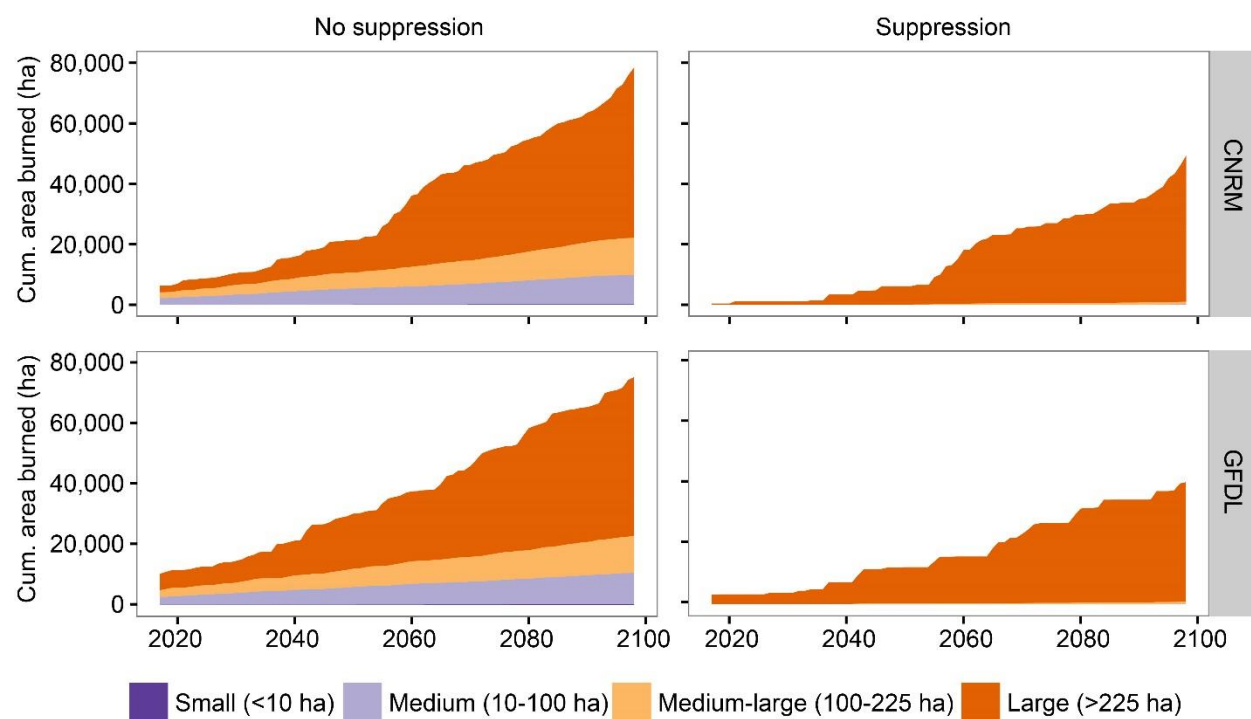


Figure 4.

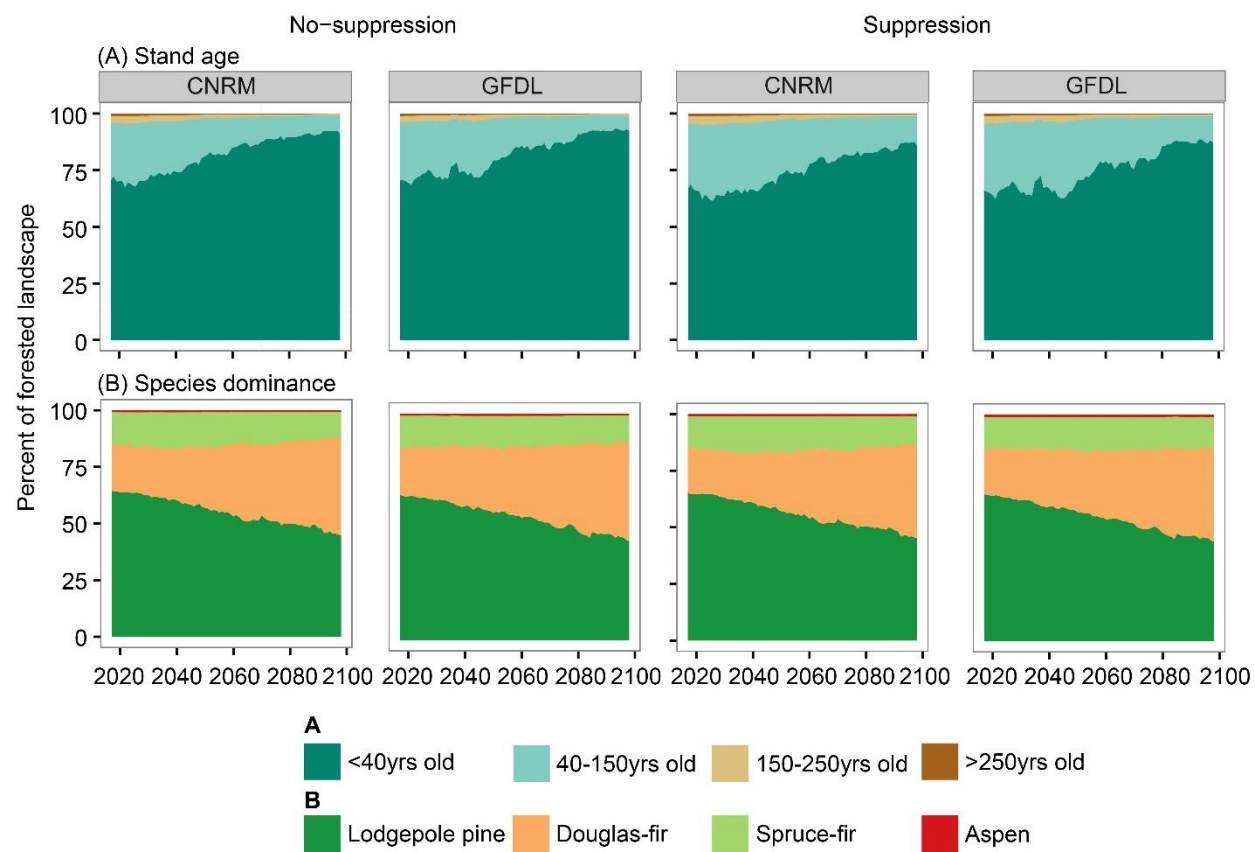
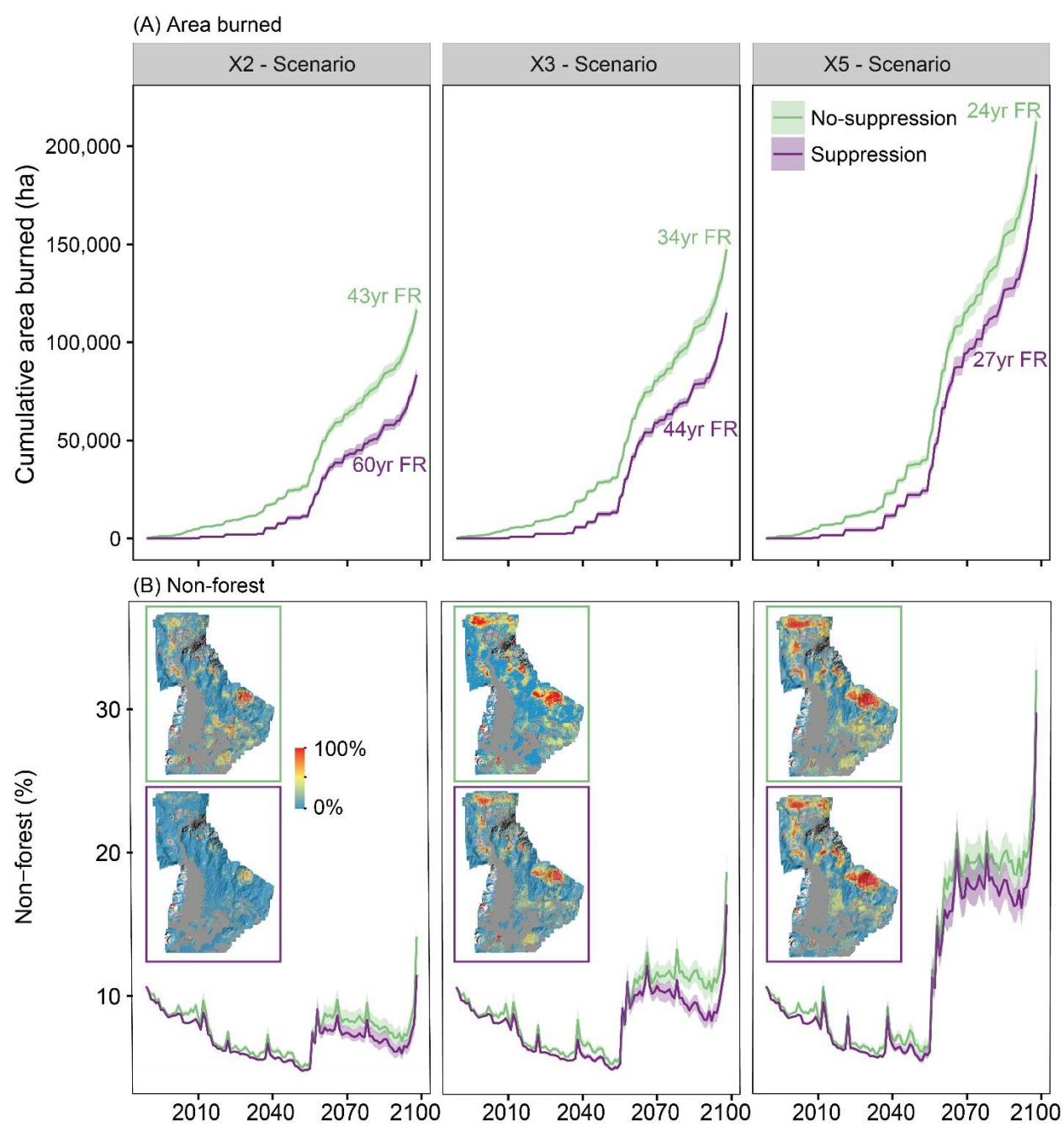


Figure 5.



## **Appendix 1 – Dynamic fire module parameterization and evaluation**

For an extended description of the iLand fire module and its structure see Seidl et al. (2014). To ensure the iLand fire module reasonably simulated fires in our study area, we calibrated key parameters and then compared simulated fires with the dynamic fire module to the historical fire record for southern Greater Yellowstone (1970-2016). For all evaluations of the dynamic fire module, we ran 20 replicate simulations under historical climate conditions (1950-2005) to account for the stochastic nature of fire events.

### *Module parameterization*

The fire extinction probability (probability of fire going out in any given cell as fire spreads across the landscape) is the key determinant of fire shape in iLand. Thus, we calibrated the fire extinction parameter in iLand to simulate fire shapes that were consistent with observed patterns in the study landscape. We iteratively ran simulations of fire spread. Then, we compared perimeter-to-area ratios of simulated and actual fire events of comparable size in the historical record. The fire extinction probability was adjusted until simulated and actual fires matched well. A total of 143 historical events were compared with 3,811 simulated fires. A fire extinction probability of 0.315 (Table 1) yielded a good fit with the historical fire record (Fig. 1).

We then parameterized the coefficients that determine tree crown kill as a function of available fuel, tree DBH, and bark thickness. In turn, these parameters determine the proportion of a fire event that burns as stand replacing (> 90 % of mature trees killed). In subalpine forest of the Northern Rocky Mountains, an average of 38% of the area within the perimeters of large fires (>250 ha) burned as stand replacing between 1984 and 2010 (Harvey et al. 2016). We calibrated the parameters controlling tree crown kill by iteratively running fire spread

simulations using historical climate (as above) and comparing the simulated proportion of stand-replacing with that reported by Harvey et al. (2016). In our simulations, an average of  $39\% \pm 1\%$  of the area within fire perimeters burned as stand replacing, and that percentage increased with fire size (Fig. 2). The final parameter set for the dynamic fire module is presented in Table 1.

### *Module evaluation*

We then evaluated how the number of fires, fire patch sizes, and annual area burned in our study area using the dynamic fire module compared to the historical record. In our study area, historical fire perimeters incorporate both forest and non-forest. In contrast, iLand only simulates fire in forests. To ensure accurate comparisons, we ran a 47-year simulation (length of the historical fire record) of our study area where we deterministically implemented the fire perimeters from the historical record using a cookie-cutter approach. This allowed us to quantify the number of fires that ignited in forest and the area of forest that burned in each fire. We then calculated the number of fires  $\text{yr}^{-1} > 0.04\text{ha}$  (fire pixel size in iLand), the number of large fires  $\text{yr}^{-1}$ , and area burned  $\text{yr}^{-1}$  (Table 2). We then ran 20 replicate simulations using the dynamic fire module and calculated the same metrics ( $n = 20$ ). We also compared individual fire event sizes between the historical ( $n = 91$  fires) and the dynamic simulations ( $n = 3,876$ ).

iLand simulations using the dynamic fire module generally aligned with the simulation using historical fire records (Table 2). On average, the dynamic fire module modestly overestimated the number of fires  $> 0.04\text{ ha}$  that occurred and slightly under-estimated the number of large fires. However, area burned per year agreed well. In the historical simulation, mean fire size was  $84\text{ ha} \pm \text{SD } 434\text{ ha}$  and ranged from  $0.04\text{ ha}$  to  $3,915\text{ ha}$ . Fires from the dynamic fire module averaged  $48.5\text{ ha} \pm \text{SD } 71.8\text{ ha}$  and ranged from  $0.04\text{ ha}$  to  $725\text{ ha}$ . The over estimation

of the number of fires greater than 0.04 ha makes sense because the dynamic fire module does not include any fire suppression, and up to 60% of fire starts have been suppressed in the real landscape during this time period. In the historical simulation, many fires were excluded because they were suppressed when they were very small (Fig. 3A). The underestimation of annual area burned in the dynamic fire module is related to the occurrence of very large fires. In the historical simulation, one ~ 4,000 ha fire occurred (Fig. 3B). While it is statistically possible for a similar sized fire to occur in the dynamic fire simulations, it is by nature, extremely rare and did not occur.

### **Literature cited**

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Table 1. Parameters and their values for the dynamic fire module. Some parameter values vary spatially on a 1 ha resolution grid. Dim=dimensionless.

Parameter	Unit	Value
<i>Ignition, fire size, fire spread</i>		
Reference Keetch Byram Drought Index	dim	Spatially variable
rFire Suppression	dim	1
Mean annual precipitation	mm	1,300
Mean fire patch size	ha	75
Minimum fire patch size	ha	1
Maximum fire patch size	ha	20,000
Fire size sigma	dim	0.5
Fire return interval	year	45
Fire extinction probability	dim[0,1]	0.315
Minimum wind speed	m s <sup>-1</sup>	10
Maximum wind speed	m s <sup>-1</sup>	30
Dominant wind direction	degrees	225
<i>Fire severity</i>		
Fuel a	*	0.8
Fuel b	*	0.2
Fuel c	*	0.4
Crown kill a	#	0.04325
Crown kill b	#	-0.001



Canopy dbh	cm	25
Soil organic matter consumed	dim[0,1]	0.02
Foliage consumed	dim[0,1]	0.9
Branch consumed	dim[0,1]	0.5
Stem consumed	dim[0,1]	0.1

\* Empirical parameters to calculate available fuel accounting for moisture, # Empirical

parameters to calculate percent crown kill from available fuels, mean tree dbh, and bark

thickness

Table 2. Descriptive statistics comparing a simulation where historical fire perimeters were implemented ( $n = 1$ ) and 20 replicate simulations using the dynamic fire module ( $n = 20$ ) for fires  $\geq 0.04$  ha.

	Historical file	Dynamic fire module			
	( $n = 1$ )	( $n = 20$ )			
		Mean	SD	Min	Max
Number of fires per year	1.9	3.5	0.17	3.15	3.9
Number of large fires (> 300 ha) per year	0.085	0.06	0.02	0	0.091
Area burned per year (ha)	163	171	17.4	139	197

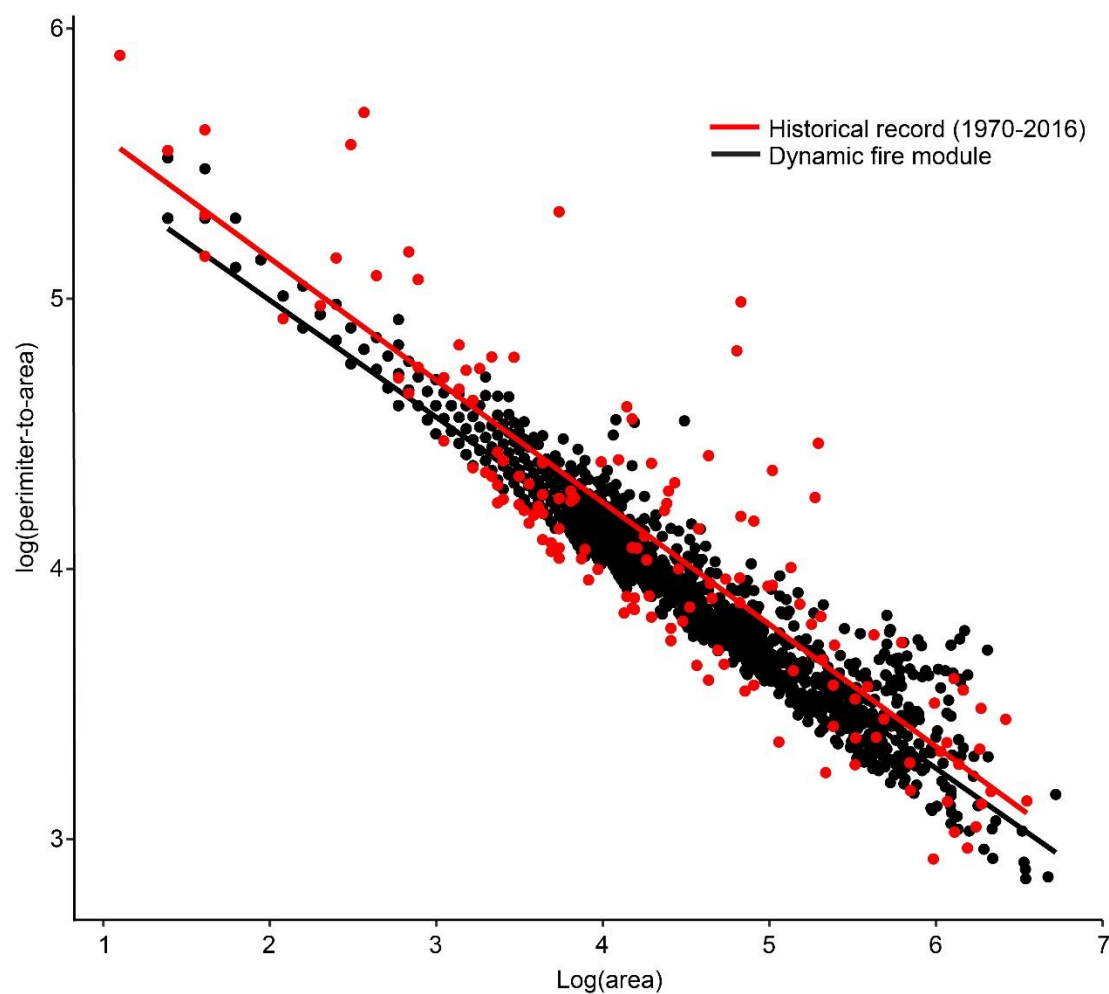


Figure 1. Fire event perimeter-to-area ratio as a function of fire event size. Red dots are fire events from the historical record (1970-2016) and the line show a linear fit. Black dots are fire events simulated under historical climate (1950-2005) using the dynamic fire module and the line shows the linear fit.

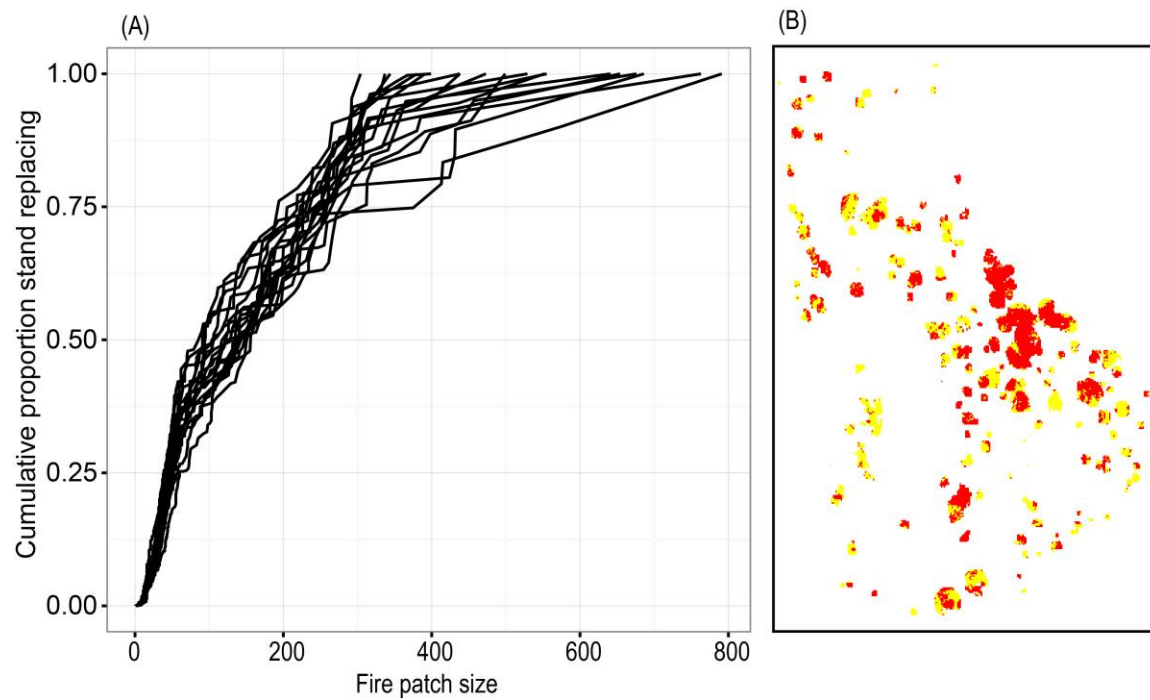


Figure 2. (A) Cumulative proportion of stand replacing burned area as a function of fire event size for 20 replicate simulation runs under historical climate conditions using the dynamic fire module. (B) Map showing burn perimeters and areas that burned as stand replacing (red) or less than stand replacing (Yellow) in one of the 20 replicates.

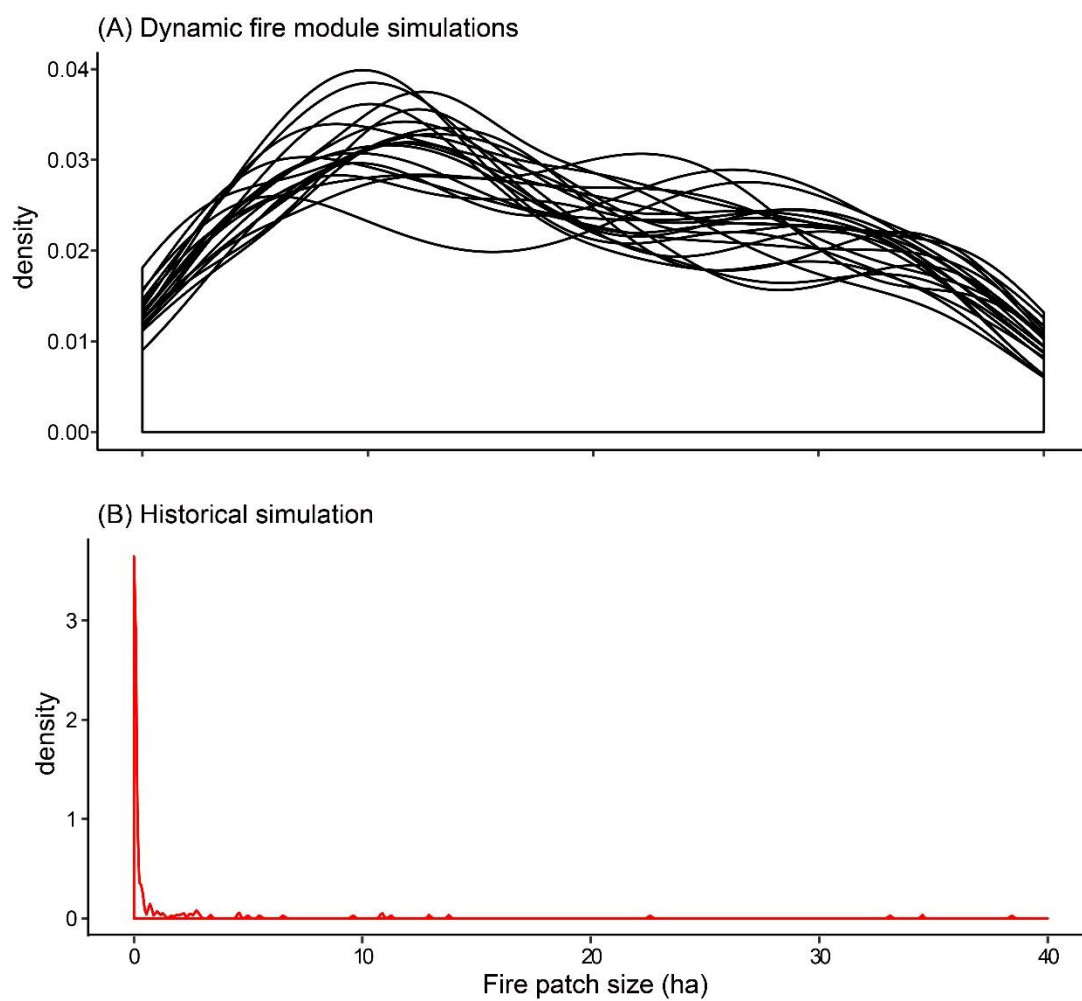


Figure 3. Fire size distributions for the 20 replicate runs with the dynamic fire module (black) and the historical fire simulation (red). Note the x axis is truncated to for visual purposes.

## **Appendix 2 -Initial conditions of spin up and landscape evaluation**

### *Initial tree species composition and stand structure*

We initialized our spin up landscape by using field inventories of early postfire stands (23-yr old) for tree species found in the study area (Donato et al. 2016, Harvey et al. 2016, Turner et al. 2016). These data were collected to cover the range of postfire stand densities and structures that commonly occur in Greater Yellowstone. We used maps of vegetation type from the National Park Service to determine where different forest types should be located in our simulated landscape (Fig. 1). We then randomly assigned a field-surveyed stand of appropriate forest type to each iLand pixel. All lodgepole pine stands above 2,400m were assigned as non serotinous and lodgepole pine stands below 2,400 m were assigned as serotinous, consistent with field observations in Greater Yellowstone (Schoennagel et al. 2003). All stand ages were artificially set to 23-yr old and tree heights were adjusted to just under 4 meters to reduce competitive effects resulting from different ages and sizes of trees in the collected field data. Original stand densities were retained. Densities for lodgepole pine ranged from 1 to 36,236 stems  $\text{ha}^{-1}$ , Engelmann spruce/subalpine fir densities ranged from 1 to 1,056 stems  $\text{ha}^{-1}$ , Douglas-fir densities varied between 1 and 1,927 stems  $\text{ha}^{-1}$ , and aspen densities ranged from 1 to 411 stems  $\text{ha}^{-1}$  in year zero of the spin up.

### *Soil characteristics and carbon pools*

iLand requires spatially explicit information on soil texture (% sand, % silt, % clay), relative soil fertility (0 – 100 scale), and effective soil depth. Soil depth and texture for the simulated landscape were extracted from CONUS, a gridded soil-characteristics database (1-km grid cell size) derived from the USDA State Soil Geographic Database (STATSGO) and

designed for modeling applications ([http://www.soilinfo.psu.edu/index.cgi?soil\\_data&conus](http://www.soilinfo.psu.edu/index.cgi?soil_data&conus)). CONUS stratifies soil into several different depth layers. We calculated average soil texture in each pixel across all depth layers to provide a single value.

To calculate relative fertility, we used a geological map of parent material in Greater Yellowstone and US Forest Service Forest Inventory and Analysis plots where lodgepole pine was the dominant tree species. We assigned pixels underlain by rhyolite parent material a relative-fertility value of 45, which we know appropriately represents edaphic effects on forest succession from extensive calibration and testing. We then used differences in lodgepole pine site index (as measured in Forest Inventory and Analysis plots) between stands located in areas underlain with rhyolite and stands underlain by other parent materials to assign relative-fertility values. Relative fertility varied between 45 and 59 across six different parent materials found in the study area.

Initial forest floor carbon pools (litter, downed wood) were assigned based on an extensive chronosequence conducted in lodgepole pine stands of Yellowstone that estimate carbon pools for stands of varying density and age class (Kashian et al. 2013). In the Rocky Mountains, carbon pools have been shown to not differ in stands with different dominant conifers (Bradford et al. 2008), and thus, we felt comfortable using estimates from lodgepole pine stands to initialize carbon pools. Initial values were 40,160 kg C ha<sup>-1</sup> of coarse downed wood, 6,142 kg C ha<sup>-1</sup> of litter and 3,888 kg C ha<sup>-1</sup> of soil organic matter carbon.

### *Climate*

We used a historical climate record (1950-2005) from a downscaled (4-km resolution) General Circulation Model (CNRM-CM5) that is known to accurately represent historical

conditions in Greater Yellowstone (See methods section of main paper for further details).

Climate years were randomly sampled with replacement from the 55-yr record during the spin up.

### *Historical wildfire regime*

We represented the historical fire regime in the spin up using a cookie-cutter approach. During the first 282 years of the simulation, for which records of fire perimeters are not available, we used statistical distributions of fire frequency and size to determine when fires would occur and how large they would be. Probability of fire start  $p$  was modeled as:

Eqn. 1

$$p = \frac{1}{FRI * s}$$

Where  $FRI$  = the fire return interval (set at 75 years) and  $s$  = mean fire size (set at 96 ha). The probability was then compared to a random number generator to determine starts. Once a fire started, a size for the fire was drawn from a negative log-normal distribution. An actual fire perimeter of corresponding size from the historical record (1970-2016) was selected and then randomly implemented on the simulated landscape. All trees, saplings, and seedlings within the fire perimeter were killed and 90% of stem carbon from killed trees was transferred to snags and 5% was transferred to the soil pool. Five percent of the killed trees' branch carbon was transferred to soil and 40% was transferred to snags. The remainder was assumed lost to the atmosphere. Serotinous lodgepole pine released their seeds and aspen resprouted following simulated fires. For the final 18 years of the spin up we implemented actual fire perimeters from the historical record.



### *Initial landscape evaluation*

To ensure we started scenarios with a simulated landscape that was representative of current forest conditions, we conducted a series of tests on the spin up landscape in year 300 to characterize forest stand structure and tree species composition, and carbon pools.

### *Forest stand structure and tree species composition*

In simulation year 300, stand density averaged 6,875 stems  $\text{ha}^{-1}$  and ranged from 0 to 393,945 stems  $\text{ha}^{-1}$ . Basal area for trees taller than 4 m averaged 17.6  $\text{m}^2 \text{ha}^{-1}$  and ranged from 0 to 47.3  $\text{m}^2 \text{ha}^{-1}$ . Both stand densities and basal areas are comparable to forest surveys characterizing stand structure in subalpine forests of Greater Yellowstone (Turner et al. 2016, Donato et al. 2016, Kashian et al. 2005). In year zero, lodgepole pine trees were present in 76% of forested pixels, Engelmann spruce and subalpine fir were present in 42% of forested pixels, Douglas fir trees were present in 25% of forested pixels and aspen were present in 3% of forested pixels (Fig. 2). By year 300, Lodgepole pine were present in 92% of forested pixels, Engelmann spruce and subalpine fir were present in 61% of forested pixels, Douglas-fir were present in 46% of forest pixels and aspen trees were present in 4.2% of forested pixels. In year 300, stand age averaged 63 years and ranged from 1 year to 323 years (Fig. 3).

### *Carbon pools*

In simulation year 300, snag carbon pools averaged  $19,817 \pm 70 \text{ kg ha}^{-1}$ , coarse wood averaged  $46,862 \pm 96 \text{ kg ha}^{-1}$ , and litter averaged  $8,440 \pm 24 \text{ kg ha}^{-1}$ . These values are generally comparable to a chronosequence measuring carbon pools in lodgepole pine forests of varying age classes (Kashian et al. 2013).

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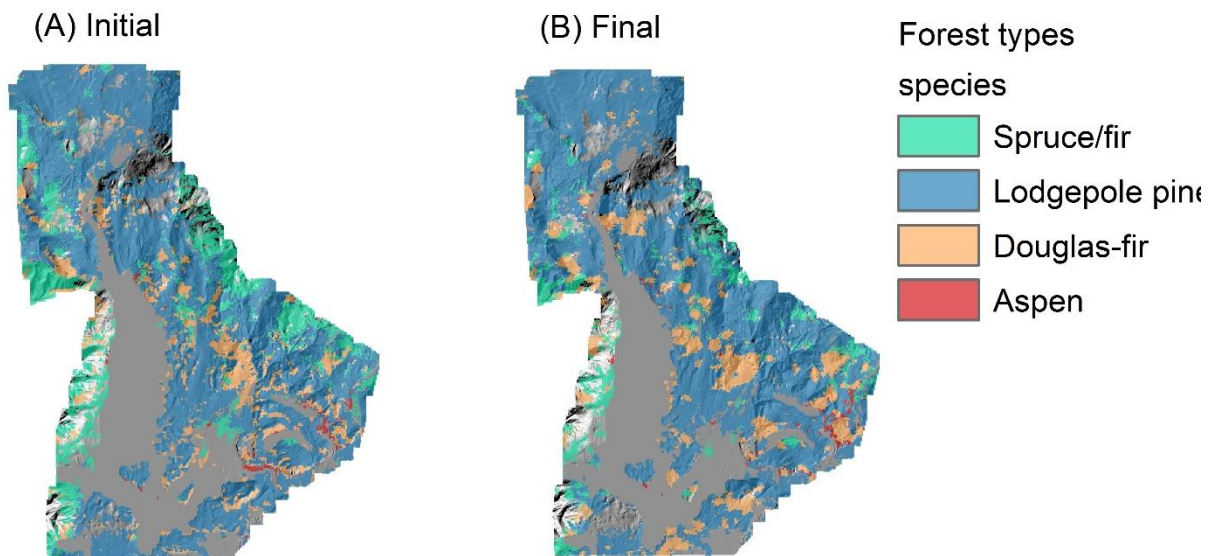
**Figures**

Figure 1. (A) Initial forest-type dominance determined by species importance values. Initial classification was based on a National Park Service vegetation type map. (B) Forest-type dominance in simulation-yr 300. The final landscape of the spin up was then used in scenarios.

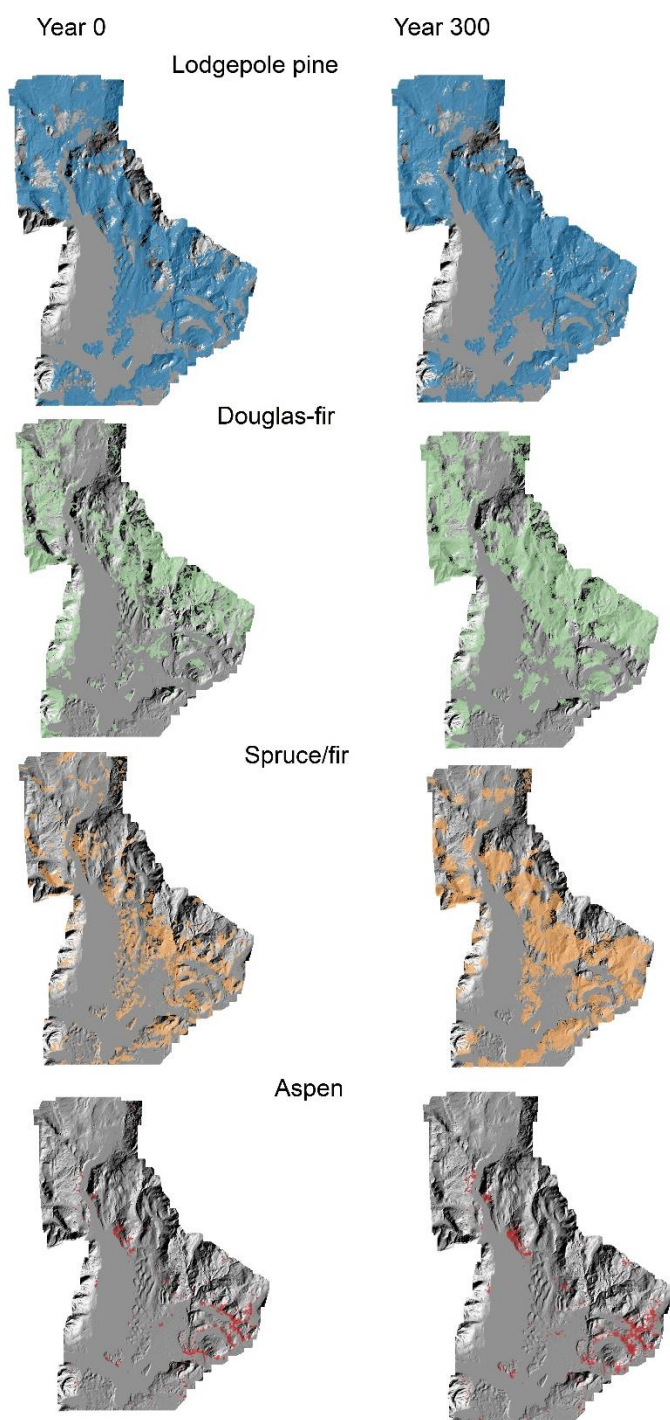


Figure 2. Presence of lodgepole pine, Engelmann spruce/subalpine fir, Douglas-fir, and aspen in simulation year 0 and simulation year 300.

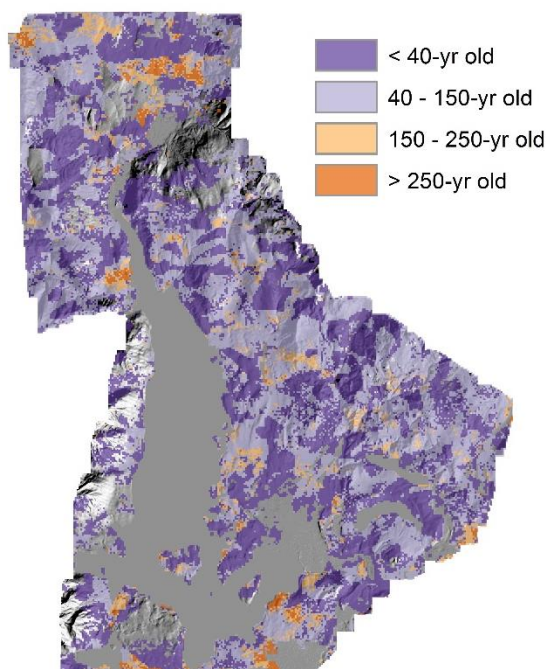


Figure 3. Stand-age distribution in simulation year 300

## Dissertation Conclusion

How rapidly changing climate and disturbance regimes will alter earth's forests in the 21<sup>st</sup> century remains unresolved but critically important (Johnstone et al. 2016, Ghazoul and Chazdon 2017). In this research, I used field observation, experiments, and computer simulations to quantify effects of changing climate and disturbance on postfire regeneration, a critical life history stage, in subalpine conifer forests of Yellowstone (Jackson et al. 2009, Walck et al. 2011). This dissertation demonstrates that multiple approaches can and must be integrated to quantify forest resilience, better anticipate whether and why abrupt changes may occur, and inform more nuanced forest management. Some key findings of the research are summarized below.

### 1. **Climate change and disturbances can initiate rapid shifts in species distributions**

**over relatively short periods.** We generally consider changes in tree-species distributions as a slow process because trees are long lived, immobile, and dispersal often occurs over relatively short distances. However, disturbance events, like the 1988 Yellowstone fires, can be powerful forces for reorganization, facilitating colonization by tree species that best match current conditions and extirpating species that no longer can establish. Continued warming is likely to increase the prevalence of these post-disturbance reorganization events.

### 2. **Warming and drying may strongly reduce post-disturbance tree regeneration, but**

**their effects will likely be contingent and difficult to predict.** Subalpine conifer seedlings are extremely sensitive to environmental conditions. I identified a range of just 5.5 °C in which seedling establishment reliably occurred. Across that range, the effects of warming changed fundamentally. This highlights the importance of considering warming

and drying trends on seedling establishment within a broader context that accounts for mediating influences of elevation, topography, aspect, and substrate.

**3. At broader scales and over longer periods, subalpine forests could prove remarkably**

**resilient to projected changes in climate and fire.** In simulated stands, I found regeneration failure to be the exception rather than the rule, and multiple climate-fire drivers were often necessary for regeneration failure to occur. At broader scales, my simulated subalpine landscape remained largely forested through the end of the 21<sup>st</sup> century even under the most extreme climate-fire projections. It seems unlikely that regional conversion of subalpine forests to non-forest will occur. Instead, landscape heterogeneity may coarsen with non-forested areas beginning to emerge in the middle of large burned patches and on south facing slopes.

**4. . Fire suppression will likely have little impact on 21<sup>st</sup>-century fire or forests.**

Fire suppression reduced burned area but did not alter 21<sup>st</sup>-century fire trends or forest landscapes. These results suggest that rapid increases in fire activity are likely inevitable but managers could have tremendous flexibility to strategically suppress 21<sup>st</sup>-century subalpine fire, given appropriate weather, without worrying that current actions will affect subsequent fire or forest landscapes. However, the window for even strategic fire exclusion may be closing, as conditions become hotter and drier and more fires grow large, making them impossible to suppress.

My master's advisor once told me: *The more you learn, the more you should realize that you will always be standing on the shores of the unknown.* In that spirit, I also highlight some of the interesting questions that arose from this research.

#### Tree regeneration

1. How do intraspecific and interspecific variation in traits mediate effects of drought on seedling establishment, survival, and growth, and what are the relative contributions of genetics versus plasticity in driving this variation?
2. How do interspecific and intraspecific competition mediate establishment, survival, and growth of seedlings, and how might competition between individuals ultimately shape species distributions?
3. How might effects of edaphic conditions change as trees grow from juvenile to adult stages, and are there substrate types where establishment is possible but subsequent survival is not?

#### Forest resilience and management

4. How can we anticipate vulnerability points in forest successional trajectories, and how do those vulnerability points vary across the western United States?
5. How can we begin to disentangle legacy effects of fire suppression versus climate change in forest ecosystems where suppression strongly influences the fire regime, and how might pulling those threads apart alter 21<sup>st</sup>-century projections of fire activity and forest resilience?



6. How can we develop more anticipatory management strategies or repurpose current strategies to account for cross-scale interactions and nonlinear feedbacks in hierarchically organized forest systems that are experiencing rapid environmental change?

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